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Neogene Paleontology in the northern Dominican Republic

4. The Genus *Stephanocoenia* (Anthozoa: Scleractinia: Astrocoeniidae)
by
Ann Budd Foster

5. The Suborders Caryophylliina and Dendrophylliina (Anthozoa: Scleractinia)
by
Stephen D. Cairns and John W. Wells

6. The Phylum Brachiopoda
by
Alan Logan

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NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC

4. The Genus *Stephanocoenia* (Anthozoa: Scleractinia: Astrocoeniidae)

By

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ABSTRACT

Multivariate statistical procedures are used to distinguish species in the reef-coral genus *Stephanocoenia* through a continuous Neogene sequence (five-million year time interval) in the Cibao Valley of the northern Dominican Republic. This genus is the only member of the family Astrocoeniidae that occurs in the sequence. The material consists of 56 colonies (17 of which are measured) from 24 localities in four river sections, the most important being Río Gurabo and Río Cana. Ten characters are measured on each of 10 corallites per colony. The data are analyzed using cluster and canonical discriminant analysis to group colonies into clusters representing species. Identical measurements on modern colonies collected near Discovery Bay, Jamaica are included for comparison. Two fossil species are defined in the analysis, one of which is new (*Stephanocoenia duncani,* n. sp.). Both species are significantly distinct from the single modern species (*S. intersepta*) that is the sole living representative of the genus. Study of collections from other reef localities shows that both fossil species occur only during Neogene time and only at a limited number of localities.

Patterns within each species are traced up a composite stratigraphic section using nonparametric statistical analyses. One of the two fossil species (*S. spongiformis*) is found to remain stable through time, whereas the other (*S. duncani*) changes its morphology in a direction approaching the cluster for the modern species. Further study of patterns of variation within the one modern and two fossil clusters shows that intraspecific variation is unusually complicated in this genus. The clusters overlap, and colonies within each cluster differ widely. Variation between populations within the modern species occurs in the same characters as those which distinguish the modern species from the fossil species converging with it (*S. duncani*). However, these two species form a morphologic continuum that cannot be explained by environment alone. Therefore, they may represent two gradually intergrading chronospecies within one lineage.

Of the two fossil species of *Stephanocoenia* defined, one species (*S. spongiformis*) exhibits an evolutionary pattern similar to that observed in the family Poritidae. In this pattern, species were found to have short durations and stable morphologies and to have become extinct during the mid- to late Pliocene through early Pleistocene mass extinction. In contrast, the second species of *Stephanocoenia* (*S. duncani*) may have evolved over a long time period, possibly forming chronospecies that survived the mass extinction. Unlike genera in the Poritidae, however, no radiation of taxa occurred in the genus after the extinction event. Since no consistent relationship has been discovered between morphology and environment in these corals with the data at hand, their paleoecologic value can only be determined after data on more taxa are collected, and their associations with other corals are studied. This study represents part of a multidisciplinary project on the stratigraphy and paleontology of the northern Dominican Republic, coordinated by P. Jung and J. B. Saunders of the Naturhistorisches Museum Basel, Switzerland.

RESUMEN

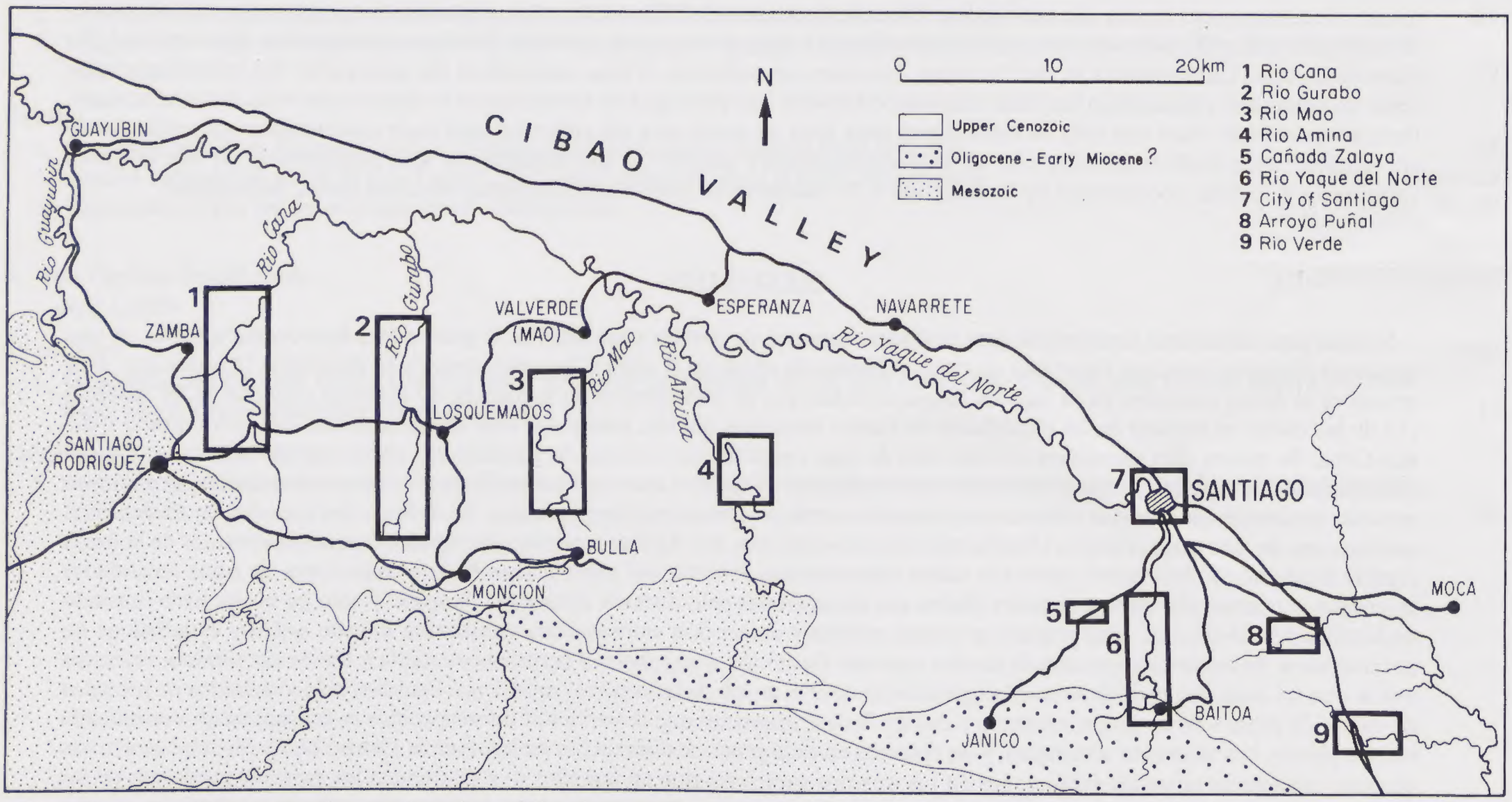
Se usan procedimientos estadísticos para distinguir especies de corales arrecifales en el género *Stephanocoenia* a travéz de una secuencia Neogéna contínua (intervalo de cinco millones de años) en el valle Cibao del norte de la República Dominicana. Este género es el único miembro de la familia Astrocoeniidae que se encuentra en la secuencia. El material consiste de 56 colonias (17 de las cuales se miden) de 24 localidades en cuatro secciones del río, siendo las mas importantes las del Río Gurabo y del Río Cana. Se miden diez caracteres en cada una de diez coralitas por colonia. Se analizan los datos usando análisis canónicos discriminatorios y de grupo para combinar las colonias en conjuntos que representen especies. Para compararlas, se incluyen colonias modernas de medidas idénticas recolectadas cerca de Discovery Bay, Jamaica. Se definen dos especies de fósiles en el análisis, una de las cuales es nueva (*Stephanocoenia duncani,* esp. n.). Ambas especies son significativamente distintas de la única especie moderna (*S. intersepta*), que es la única representante viviente del género. Estudios de colecciones de otras localidades de corales muestran que ambas especies fósiles son encontradas solo durante el tiempo Neogéno y solo en un numero limitado de localidades. Dentro de cada especie se trazan modelos de sección estratigráfica compuesta usando análisis estadísticos no paramétricos. Se encuentra que una de las dos especies fósiles (*S. spongiformis*) permanece estable a travéz del tiempo, mientras que la otra (*S. duncani*) cambia su morfología acercandose al grupo de las especies modernas. Estudios más avanzados de modelos de variación dentro de un grupo moderno y dos de fósiles, muestran que la variación intraespecífica es inusualmente complicada en este género. Los grupos se translapan, y las colonias en cada grupo se diferencian ampliamente. Dentro de las especies modernas ocurren variaciones entre las poblaciones en los mismos caracteres que en aquellos que distinguen las especies modernas de las especies de fósiles que convergen en ella (*S. duncani*). Sin embargo, estas dos especies forman un contínuo morfológico que no puede ser explicado solamente por el medio ambiente. Por lo tanto, pueden representar dos cronoespecies que se integran gradualmente en un linaje. De las dos especies de fósiles definidas de *Stephanocoenia,* una especie (*S. spongiformis*) exibe un

modelo evolucionario similar a aquel observado en la familia Poritidae. En este modelo, se encontraron que las especies tienen duraciones cortas y morfologías estables y que se extinguieron durante el medio a tarde Plioceno a travéz de destrucciones masivas en el Pleistoceno temprano. En contraste, la segunda especie de *Stephanocoenia* (*S. duncani*) puede haber evolucionado en un periodo de tiempo largo, posiblemente formando cronoespecies que sobrevivieron la destrucción masiva. Sin embargo, en forma diferente al género de Poritidae, no ocurrió ninguna radiación de taxa en el género despues de la destrucción. Ya que con los datos a mano no se descubrió ninguna relación consistente entre la morfología y el medio ambiente, su valor paleocológico se puede determinar solamente luego de haber coleccionado mas datos en taxa, y luego de haber estudiado sus asociaciones con corales. Este estudio representa parte de un proyecto multidisciplinario en la estratigrafía y paleontología del norte de la República Dominicana, coordinado por P. Jung y J. B. Saunders del Naturhistorisches Museum Basel, Suiza.

INTRODUCTION

The purpose of this paper is to describe the species of one coral family (herein represented by only a single genus) in one region by quantitative study of populations collected at closely-spaced stratigraphic intervals, and to trace their evolutionary patterns over a five- to ten-million year time segment, following the major coral extinction event that occurred during late Oligocene and early Miocene time. This paper is the second in a series of coral faunal descriptions for the middle Miocene to middle Pliocene of the northern Dominican Republic. It deals with a common but little-studied coral genus, *Stephanocoenia* Milne-Edwards and Haime, 1848a, a mound-shaped coral, sometimes large in size, that represents an important reef-building component in the Caribbean from middle Miocene to modern time. As in the first paper (Foster, 1986), the coral collections in this study were made stratigraphically in bulk between 1978 and 1980 by J. Geister, P. Jung, J. B. Saunders and coworkers as part of their large-scale multidisciplinary project on the paleontology and stratigraphy of the Cibao Valley of the northern Dominican Republic. The project has focussed on this region because it contains one of the richest, most continuous, and best-studied sections through Neogene fossiliferous units in the Caribbean. All collecting localities are keyed into their detailed stratigraphic sections (Saunders, Jung, and Biju-Duval, 1986). The coral faunal descriptions are part of a series of papers on these collections, planned to cover all fossil taxa occurring in the sections.

Previous work on the systematics of the Neogene Dominican Republic corals has been reviewed in Foster (1986). In this work on the Dominican Republic, the genus *Stephanocoenia* is only rarely mentioned. Duncan (1863, 1864, 1868) described only two species of *Stephanocoenia* in the Heneken collection at the British Museum (Natural History), London, England, U.K. [BM(NH)]. They are *Stephanocoenia intersepta* (Esper, 1795) and *Plesiastraea spongiformis* Duncan, 1864. Pourtalès (1875) listed only one species, *S. intersepta*



Text-figure 1.—Map indicating the location of the river sections sampled. *Stephanocoenia* was found only in four sections: (1) Río Cana, (2) Río Gurabo, (3) Río Mao, and (4) Río Yaque del Norte (map from Saunders, Jung, and Biju-Duval, 1986).

(Esper, 1795). Similarly, Vaughan (1919, and an undated unpublished manuscript) synonymized Duncan's two species and indicated that only one species of *Stephanocoenia* [*S. intersepta* (Esper, 1795)] occurs in the Neogene of the Dominican Republic (see also Vaughan *et al.,* 1921). No species of *Stephanocoenia* were treated in Vaughan and Hoffmeister (1925) or in any other subsequent papers on the Dominican Republic corals. In all the Caribbean Miocene through lower Pliocene excluding the Dominican Republic, *Stephanocoenia* is only known in the Bowden Formation of Jamaica (Vaughan, 1919) and at St. Croix in Trinidad [Heneken collection, BM(NH)].

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ABBREVIATIONS OF REPOSITORY INSTITUTIONS

AMNH: American Museum of Natural History, New York, NY, U.S.A.
BM(NH): British Museum (Natural History), London, England, U.K.
MNHNP: Muséum national d'Histoire naturelle, Paris, France
NMB: Naturhistorisches Museum Basel, Basel, Switzerland
NMS: Natur-museum Senckenberg, Frankfurt, West Germany
UCMP: University of California Museum of Paleontology, Berkeley, CA, U.S.A.
UI: University of Illinois, Department of Geology, Urbana, IL, U.S.A.
USNM: U. S. National Museum of Natural History, Washington, DC, U.S.A.
SUI: State University of Iowa, Department of Geology, Iowa City, IA, U.S.A.

BIOSTRATIGRAPHY AND PALEOECOLOGY

The genus *Stephanocoenia* Milne-Edwards and Haime, 1848a is common in two of the river sections through the Neogene of the Cibao Valley of the northern Dominican Republic (Río Cana and Río Gurabo) that were described by Saunders, Jung, and Biju-Duval (1986). In addition, one colony was found in each of the Río Mao and Río Yaque del Norte sections. A total of 56 colonies was collected at 24 localities ranging from early Miocene to early Pliocene in age. The small size of these numbers contrasts with those for the more abundant coral family Poritidae, approximately 450 colonies of which were collected in 92 localities from the same river sections.

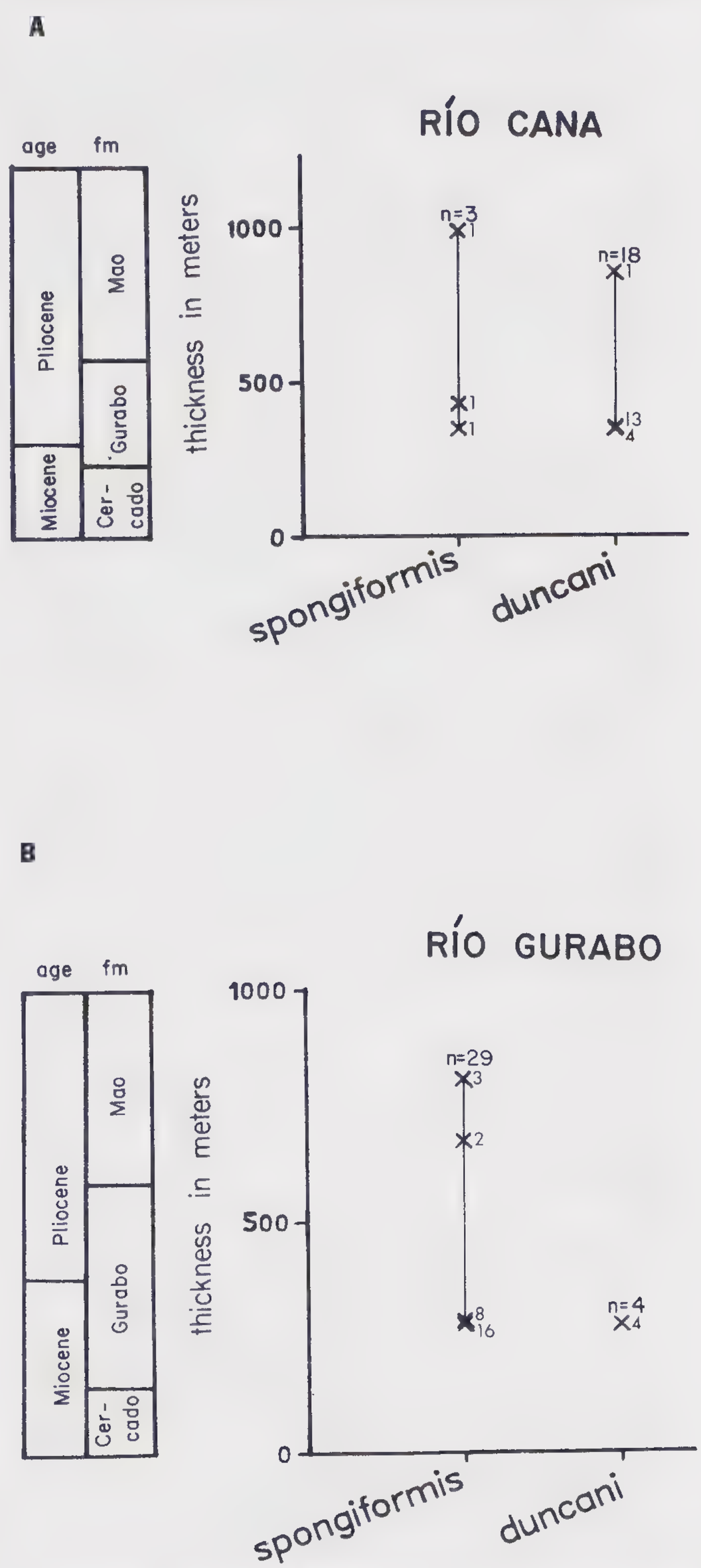
The two species represented were found in relatively equal overall abundances. Thirty-two colonies of *S. spongiformis* (Duncan, 1864) and 24 colonies of *S. duncani,* n. sp. were collected. *S. spongiformis* was more commonly found in Río Gurabo (29 colonies were collected here as opposed to only four of *S. duncani*). On the other hand, *S. duncani* was more common in Río Cana (18 colonies were collected here as opposed to only three of *S. spongiformis*). Both species exhibited wide ranges in Río Cana (Text-fig. 2A), whereas in Río Gurabo, *S. duncani* was found only at the 275 m level (Text-fig. 2B).

Little can be concluded unequivocally about the biostratigraphic or paleoecologic implications of the individual ranges of these two species. Their long du-

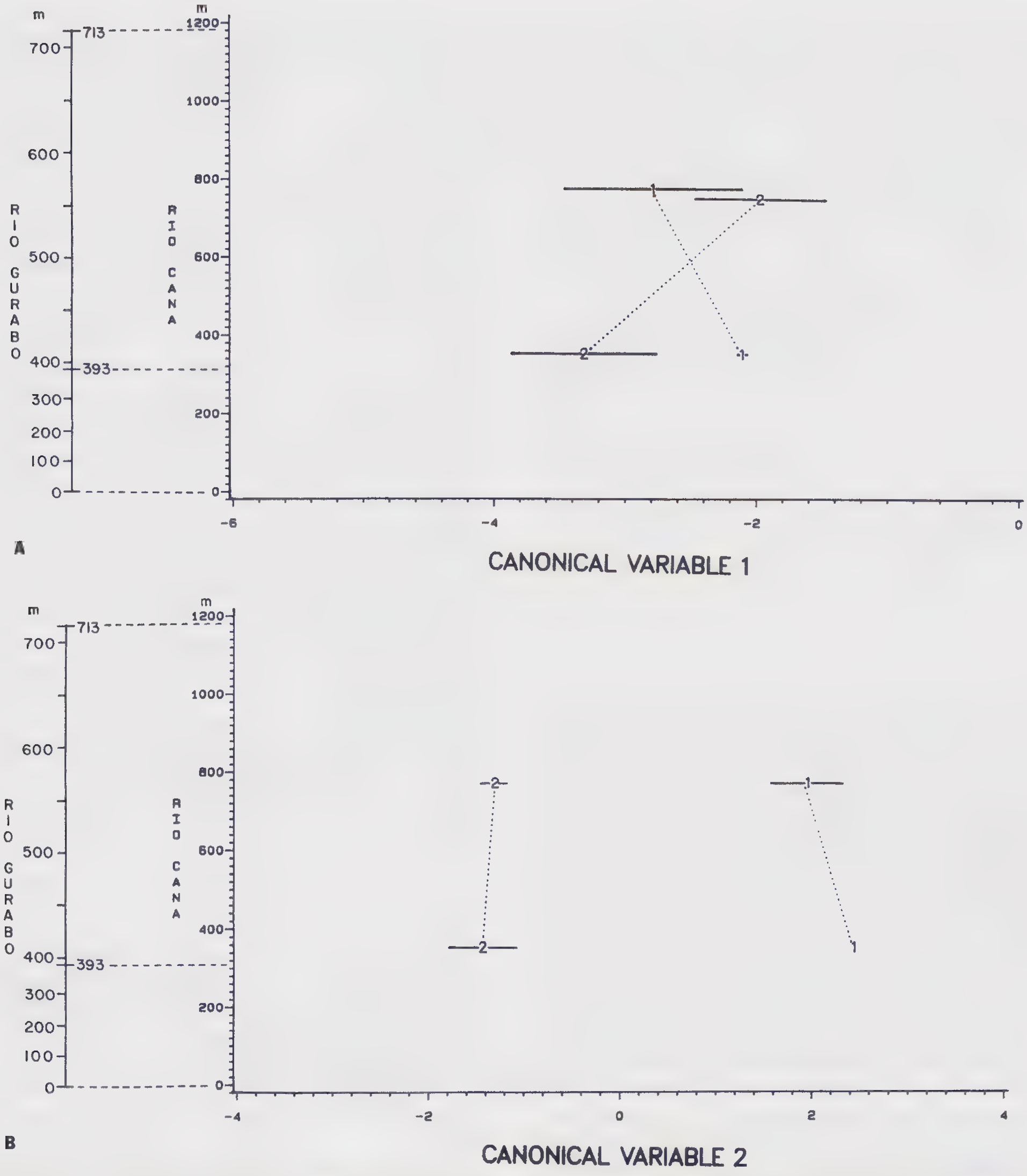
rations (approximately ten million years) and rare occurrence in other geographic areas imply they would have only limited biostratigraphic value. Neither of the two species exists today, and the only direct modern counterpart, *S. intersepta* (Lamarck, 1816) (the one living representative of the genus *Stephanocoenia*), is widely distributed both geographically across the Caribbean and ecologically from backreef lagoons to deeper areas of the forereef (Goreau, 1959; Goreau and Wells, 1967). The one fossil colony found in the older, more conglomeratic Río Yaque del Norte section of the Dominican Republic belongs to the species *S. duncani.* Assuming the shallow nearshore interpretation of Saunders, Jung, and Biju-Duval (1986) for the Río Yaque del Norte section, this information together with the restricted distribution of this species lower in the Río Gurabo section suggests that *S. duncani* might have been the older of the two species and/or that it might have occurred more commonly in nearshore habitats. Obviously, more data would be needed to substantiate these hypotheses.

Patterns of morphologic variation within species across a composite of the Río Cana and Río Gurabo stratigraphic sections (spanning a time interval of approximately five million years) show somewhat greater stability within *S. spongiformis* (Text-fig. 3). Study of Spearman's rank order correlation coefficients (SAS Inst. 1982, PROC CORR) indicates that insignificant correlations occur between morphology (canonical variables 1 and 2 of the between-species analysis described in the next section) and stratigraphic position. Intraspecific comparisons between populations (SAS Inst. 1982, PROC NPAR1WAY) collected in lower and upper stratigraphic levels (with the cutoff between "lower" and "upper" being defined at approximately the 500 m level [see Text-fig. 2]) demonstrate little difference in morphology between levels. However, in *S. duncani,* morphology appears to change upsection in a direction approaching that of modern *S. intersepta.* Comparisons between populations collected at lower and upper stratigraphic levels show a significant increase in canonical variable 1 (a variable related to inner wall and columella thickness) in *S. duncani* ($F_{(1,48)} = 12.43$; $p = 0.0009$). Nevertheless, only insignificant correlations exist between morphology and stratigraphic position.

The stability within the first species suggests not only a lack of evolutionary development, but a lack of response to large-scale environmental change, since the Río Cana and Río Gurabo sections of the Cibao Valley are believed to have been deposited under deepening environmental conditions (Saunders, Jung, and Biju-Duval, 1986). Such stability was also observed in the family Poritidae (Foster, 1986) and may be characteristic of corals that today exhibit complicated patterns of intraspecific variation which are not directly correlated with environment. The directional trend within



Text-figure 2.—Diagrams showing the distribution of species of *Stephanocoenia* within selected river sections. "n" = total number of localities containing each species. Numbers to the right of points along each vertical distribution line indicate the number of localities represented by each point. (A) Río Cana, (B) Río Gurabo.



Text-figure 3.—Variation within species in corallite characters through a composite of the Río Cana and Río Gurabo stratigraphic sections. The composite was constructed using the Río Cana section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 16) as a standard and scaling the Río Gurabo section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 6) relative to it. To accomplish this, three exact elevations were correlated between the two sections: (1) the unconformity with the Tabera Group at the base of each section, (2) the boundary between the *Globorotalia humerosa* and *G. margaritae* foraminiferal zones, and (3) the boundary between the *G. margaritae* and *G. miocenica* zones. The position of localities within each section were determined using text-figures 4 and 15 of Saunders, Jung, and Biju-Duval (1986).

The points labelled "1" and "2" on the figure represent means for all colonies within each species from each 100 meter interval along the composite section. Horizontal lines on either side of each point are one standard deviation in length. Dotted lines connect means for each species. 1 = *S. spongiformis,* 2 = *S. duncani.* (A) Canonical variable 1 of the canonical discriminant analysis between species. As described in the text, the thickness of the inner wall and of the columella are most heavily weighted on this canonical variable. Morphological change is detected in species 2, but not in species 1. (B) Canonical variable 2 of the canonical discriminant analysis between species. The spacing between corallites and development of the exothecal intercostal area are heavily weighted on this canonical variable. Morphological change cannot be detected in either species.

the second species implies gradual evolution from *S. duncani* into *S. intersepta,* signifying that the two represent merely chronospecies within one lineage. Nevertheless, on the basis of the current analyses, it is impossible completely to reject the hypothesis that morphologic change upsection in *S. duncani* is related to environment. This hypothesis is discussed in more detail in the section on intraspecific variation.

As in the family Poritidae, the potential usefulness of *Stephanocoenia* as a paleoecologic indicator can only be ascertained after all the corals in the collection of Saunders, Jung, and Biju-Duval (1986) have been studied taxonomically, and the patterns of intraspecifc variation are compared with patterns of diversity and abundance for the entire coral fauna. However, unless intraspecific trends appear to be clearly correlated with environment, data on the distribution and abundance of the two species of *Stephanocoenia* may prove more valuable in quantitative studies of species associations, especially those studies that attempt to link certain associations with particular environments (see discussion in Foster, 1986).

TAXONOMIC METHOD

PROBLEM

One genus, *Stephanocoenia,* of the family Astrocoeniidae occurs in the Neogene of the Dominican Republic. The genus occurs today only in the Western Atlantic region. Although it represents an important component of the coral fauna in lagoon through deep forereef areas, it is relatively unstudied ecologically or morphologically and is often confused with the more dominant reef-coral *Montastraea annularis* (Ellis and Solander, 1786), whose colony shape and general corallite morphology is strongly convergent with *Stephanocoenia intersepta* (Lamarck, 1816). *Stephanocoenia* differs from *Montastraea* Blainville, 1830, in its styliform columella, prominent pali, and its regular subcerioid intercostal area. Its corallites are also generally smaller than those of *Montastraea.* Similarly, fossil *Stephanocoenia* bear a striking overall resemblance to the extinct genus *Astrocoenia* Milne-Edwards and Haime, 1848a, a taxonomically more diverse genus that was especially common in the Caribbean during the Eocene and the Oligocene. *Stephanocoenia* differs from *Astrocoenia* only by having prominent pali, more septa, and a cerioid colony form. Because both genera have similar styliform columellae, this second case of resemblance is more likely truly phylogenetic.

Only one species of *Stephanocoenia* is commonly recognized in the Caribbean from Miocene (possibly Oligocene) through modern time (Frost, 1977; Zlatarski and Estalella, 1982). Some workers have suggested that a second modern species may also exist whose skeletal morphology differs from the first primarily by having smaller corallites and wider, more porous intercostal area (Goreau and Wells, 1967; J. C. Lang, oral commun., 1983). The most convincing differences, however, involve tissue coloration and other live-polyp characters. This suggestion implies that the second species could overlap in skeletal morphology with the first, especially when large populations from a range of different habitats are studied. However, the validity of this second species has never been clearly demonstrated, in part because morphologic variability is so poorly understood in the first, more common species.

Given this lack of knowledge about species of living *Stephanocoenia,* in the current study, species have been differentiated in the fossil material by grouping specimens into clusters using purely quantitative analyses of skeletal characters. To facilitate such cluster definition, direct comparisons have been made with populations of living *Stephanocoenia intersepta* collected in three different habitats near Discovery Bay, Jamaica. The specimens from the living populations have been measured using the same techniques as in the fossils, and they have been statistically analyzed together with the fossils following the procedures of Foster (1984). Obviously, such techniques ignore some potentially diagnostic soft-tissue characters. However, they do attempt to base species definitions on means and variances of known populations, two especially important parameters in the study of highly variable and possibly overlapping species.

MATERIAL

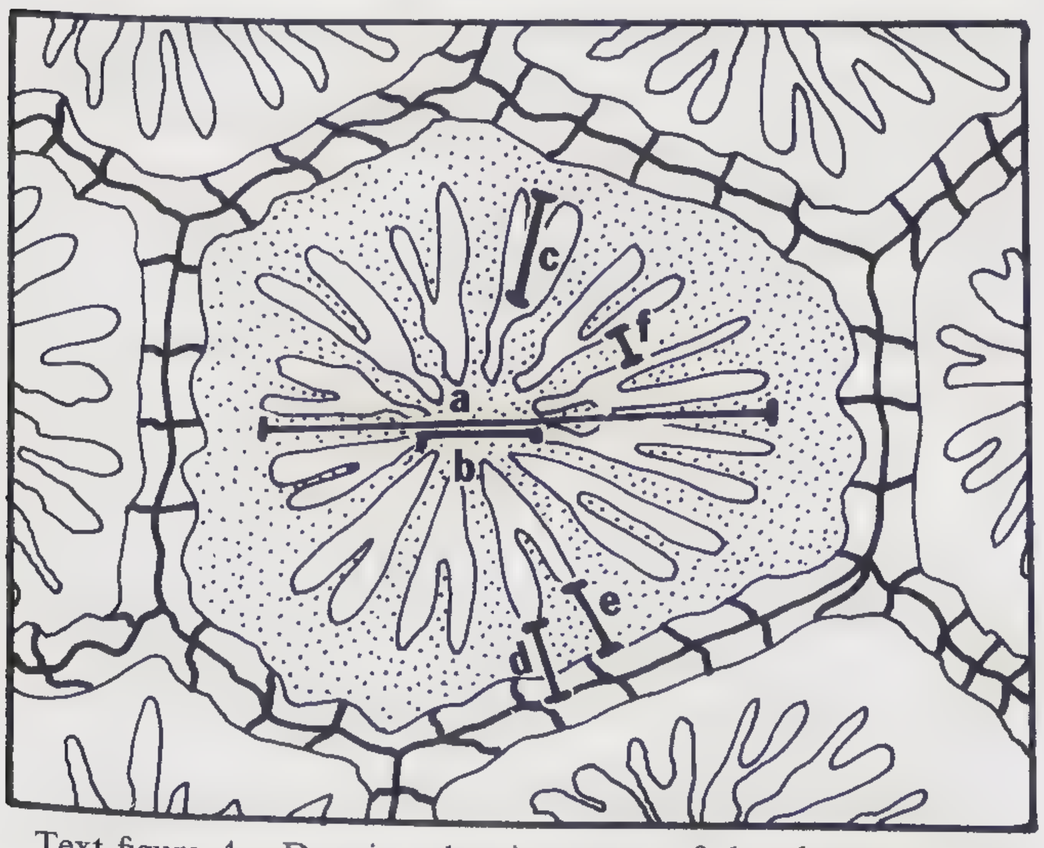
The material studied consists of all specimens of the genus *Stephanocoenia* (56 colonies) collected in the Dominican Republic by J. Geister, P. Jung, J. B. Saunders, and coworkers between 1978 and 1980. It is currently deposited at the Naturhistorisches Museum Basel. These coral collections from the Dominican Republic are termed "NMB" collections in the following discussion in order to distinguish them from material in other collections used in the analysis. All members of the family Astrocoeniidae were first sorted from the rest of the NMB collections and identified as belonging to the genus *Stephanocoenia.* The specimens were then separated into two groups, one subcerioid and the other cerioid. Eight to 10 well-preserved, larger colonies were selected from each group for thin-sectioning and measurement. One transverse and one longitudinal thin-section were prepared from near the colony surface on the top and side of each colony. Parameters were measured on thin-sections from a total of 18 NMB colonies.

Table 1.—List and description of characters measured on corallites in transverse thin-sections of *Stephanocoenia*. Characters 1 and 2 were measured to the nearest 0.04 mm and characters 3 through 7 were measured to the nearest 0.015 mm.

character	*abbreviation*	*description*
1. corallite diameter	**CD**	Linear measure across corallite center between theca/corallite cavity margins; mean of greatest and smallest lengths
2. corallite spacing	**CS**	Linear measure between centers of adjacent corallites; mean of greatest and smallest lengths
3. columella width	**CLW**	Linear measure across the columellar style; mean of greatest and smallest lengths
4. tertiary septum length	**TSL**	Linear measure from septum tip to inner thecal margin; mean of longest and shortest septa
5. total theca width	**TT**	Linear measure across entire theca from the corallite cavity margin to the center of the second wall between adjacent corallites
6. inner wall thickness	**ATT**	Linear measure across solid skeleton forming the inner wall immediately surrounding the corallite
7. septum thickness (major)	**ST**	Linear measure across major septa at septum midpoint; mean of thickest septum and next septum to its right
8. number of adjacent corallites	**NAC**	Count of corallites whose thecae abut the theca of the measured corallite
9. total number of septa	**NS**	Count of all major and minor septa
10. number of major septa	**MJS**	Count of septa extending to the columella

For comparison, 10 living colonies of *Stephanocoenia intersepta* (Lamarck, 1816) (SUI 51064–51093) were collected from each of three environmentally-distinct reef habitats near Discovery Bay, Jamaica. The habitats consisted of: (1) a nearshore turbid lagoon, 16 m depth, (2) a forereef coral thicket, 20 m depth, and (3) a forereef sand channel, 20 m depth (see Foster, 1980 for detailed locality descriptions). Transplant experiments (Foster, 1979) have shown that morphologic variation between these habitats in two other species [*Montastraea annularis* (Ellis and Solander, 1786) and *Siderastrea siderea* (Ellis and Solander, 1786)] is largely environmental. As in the fossil material, two transverse and two longitudinal thin-sections from each colony were prepared and measured.

Measurements were made only on thin-sections to insure greater accuracy and consistency of data. A total of 10 corallites was measured on each colony, since previous work (Foster, 1985) has indicated that 10 corallites per colony is an adequate sample size to estimate colony means and variances. Ten mature corallites were selected at regular intervals on each of the two transverse thin-sections per colony.



Text-figure 4.—Drawing showing some of the characters measured: (a) corallite diameter, **CD**; (b) columella width, **CLW**; (c) tertiary septum length, **TSL**; (d) total theca width, **TT**; (e) inner wall thickness, **ATT**; (f) septum thickness, **ST**.

CHARACTERS

The characters analyzed consist of linear measurements and counts on 10 corallite features in transverse thin-sections (Table 1, Text-fig. 4). All data are available on computer tape from the author. The characters were selected to include the most important diagnostic features commonly used to distinguish species in astrocoeniid corals. They can be grouped into the following categories: (1) size and arrangement of corallites, (2) development of septa, (3) thickness of septa, columellar style, and inner corallite wall, and (4) development of the intercostal area. One possibly important corallite character that was not measured is the development of the pali. In *Stephanocoenia,* the pali are not true pali (*sensu* Vaughan and Wells, 1943) formed by septal substitution, but represent thickenings of the inner margins of the major septa. They proved difficult to measure consistently in thin-section because of their often weak development and indistinct margins; therefore, they were not included in the analyses. Similarly, no whole colony measurements were included in the analyses, because preliminary observations suggested that colony shape was fairly uniform in the material studied.

A brief summary of the measured characters is given below:

1. *Size and arrangement of corallites.*—Cursory examination suggests that, after maturity, the size and shape of individual corallites remain unchanged. No clear patterns of astogeny can be deciphered. Corallites

are circular or polygonal in shape, depending on the development of the theca and the intercostal area. In general, corallites appear more circular with increased development of the intercostal area. One measure, **CD** (the mean of the long and short corallite dimensions) describes corallite size (Table 1, Text-fig. 4). Three measures, **CS**, **TT**, and **NAC**, describe corallite spacing (Table 1). The first, **CS**, is the distance between centers of adjacent corallites. The second, **TT**, is the distance across the corresponding inner walls, intercostal area and outer walls of adjacent corallites (Text-fig. 4). The third character, **NAC**, represents a count of the number of adjacent corallites.

2. *Development of septa.*—The septa are composed of six to eight vertical trabeculae that join together horizontally to form septal plates and at their outer margins to form a septothecate or parathecate wall. The septa are radially arranged into three cycles consisting of six primary, six secondary, and 12 tertiary septa. Three measures (Table 1) describe development of the septa: **NS**, the total number of septa per corallite; **MJS**, the number of septa extending completely to the columella; and **TSL**, the length of the tertiary septa (Text-fig. 4).

3. *Thickness of septa, columellar style, and inner corallite wall.*—As explained previously, the 24 septa are arranged in three cycles, with pali forming on the inner margins of the first two cycles. Costae of equal thickness extend from each septum across the septothecal inner wall immediately surrounding the corallite to a second parathecal outer wall formed at the junction between adjacent corallites (Text-fig. 4). The intercostal area between the inner and outer wall is composed of uniform, equilateral to rectangular void cells whose margins are defined by costae, inner and outer walls, and exothecal dissepiments. The double wall structure gives the coral its so-called "subcerioid" appearance in transverse section. The two walls may coalesce leaving the coral a cerioid appearance. The columella is formed by a single, prominent style, circular to elliptical in shape. The thickness of three vertical elements were measured: the major septa, **ST**; the columellar style, **CLW**; and the inner corallite wall, **ATT** (Table 1, Text-fig. 4).

4. *Development of the intercostal area.*—As explained previously, the intercostal area consists of cellular void space between the inner and outer corallite walls. The cross-sectional area of the intercostal area can be estimated using a combination of two previous measurements, **TT** and **ATT**. Therefore, no additional measures were made.

Statistical Procedures

Species were distinguished within the fossil NMB Dominican Republic *Stephanocoenia* using multivariate statistical techniques similar to those outlined in Foster (1984). The programs are contained within the computer packages SAS (SAS Inst., 1982) and SPSS-X (SPSS Inc., 1983). First, the data for each measured colony in the fossil NMB and modern Jamaican collections were analyzed using cluster analysis (SAS CLUSTER procedure, average linkage method) of principal component scores (SAS PRINCOMP procedure) (Text-fig. 5). The fossil colonies were thereby divided into two groups using a distance of 0.8 as a cutoff. The first group (*S. spongiformis*) was originally composed of six colonies; the second (*S. duncani*) of nine colonies (Text-fig. 5). The raw data were then analyzed using a series of stepwise canonical discriminant analyses (SPSS-X discriminant procedure). In the first of these analyses, the two fossil clusters and the one modern species were used to form groups, and unassigned fossil colonies were left unclassified. The results were used to assign the unclassified colonies to clusters. These clusters were then modified using subsequent canonical discriminant analyses. In this process, cluster assignments for various colonies lying at cluster margins were changed and the analyses rerun until the highest number of correctly classified corallites was obtained. Three clusters (two fossil, one modern) were finally distinguished (Table 2, Text-fig. 6).

Table 2.—Final canonical discriminant analysis of three fossil and modern *Stephanocoenia* species. Total-sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The canonical variables are labelled CV1–2. Abbreviations for characters are explained in Table 1.

original variable	CV1		CV2	
	COR	SCC	COR	SCC
CD	.306	not used	−.152	not used
CS	.391	not used	.375	not used
CLW	.512*	0.13	−.182	−0.46
TSL	.274	0.27	−.149	−0.28
TT	.320	0.06	.798*	1.04*
ATT	.840*	1.10*	−.078	−0.15
ST	.343	−0.45	−.092	0.12
NAC	.010	not used	.081	not used
NS	.026	1.35*	.120	1.23*
MJS	−.029	−1.08*	.094	−1.07*

* Most important variables.

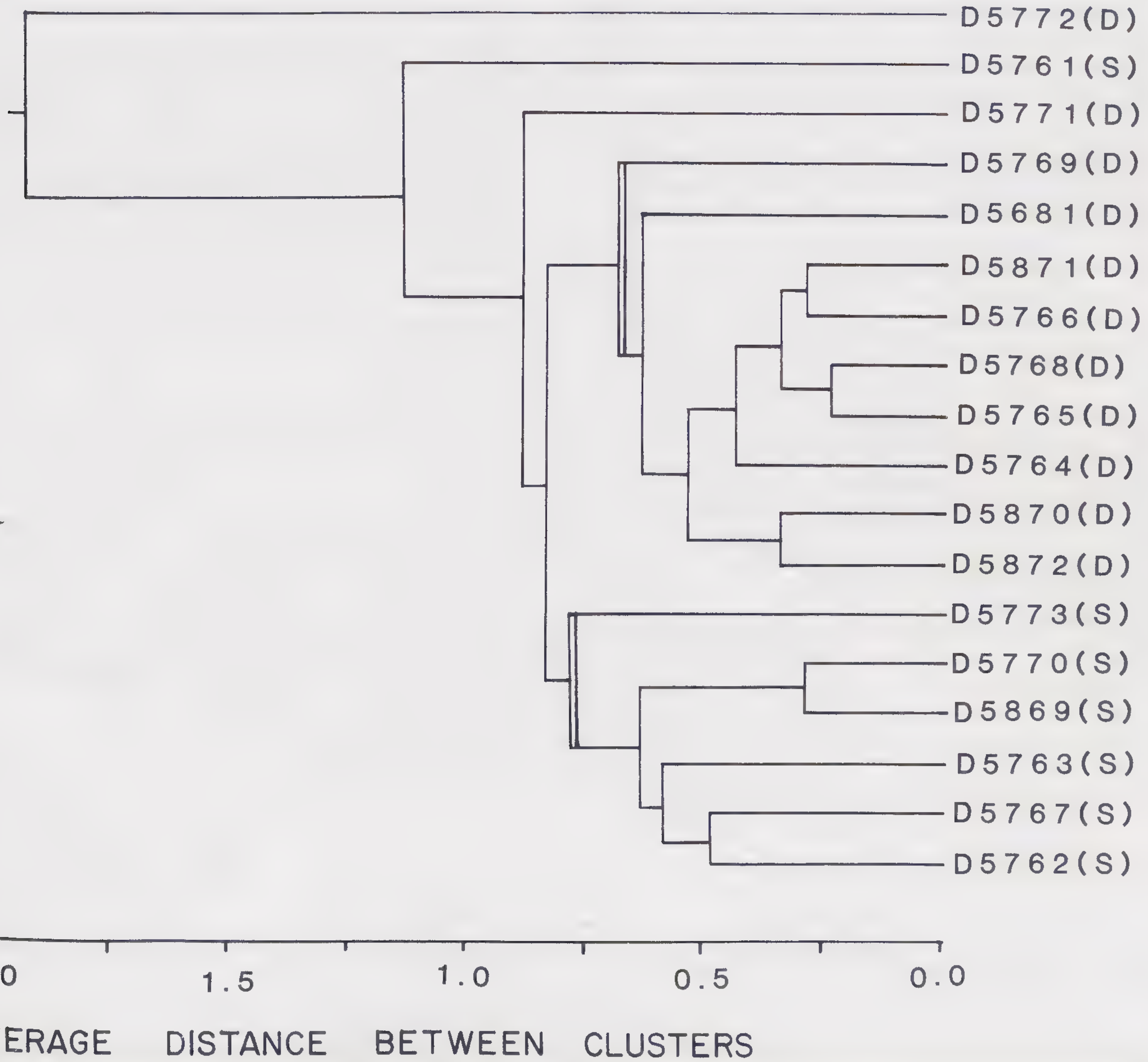
Means and standard deviations of all individual measured characters are given for the two fossil species and three modern populations in the Appendix. Six characters revealing significant differences between species are plotted in Text-figure 7.

Results and Interpretations

As described in the previous section, three clusters (two fossil, one modern) were detected in the final discriminant analysis. Of all colony means, 87.5 percent were classified correctly, with 100 percent correct

classification in the two fossil clusters and 80 percent correct classification in the modern cluster. The modern cluster (*Stephanocoenia intersepta*) overlapped most significantly with the fossil cluster described herein as a new species (*S. duncani*). As explained previously, these two clusters could be interpreted as representing chronospecies within one lineage. However, since the present results indicate that they constitute two tight clusters whose pooled variance extends beyond the limits of common phenotypic plasticity in *S. intersepta* (as estimated using the three Jamaican populations from different habitats), they will be considered separate until data on more populations suggest they form one truly continuous cluster.

Two discriminant functions were calculated in the final discriminant analysis, the first accounting for 58.66 percent of the variation and the second accounting for 41.34 percent. The first function primarily distinguishes the two fossil clusters from the modern cluster, whereas the second function distinguishes between the two fossil species. Seven of the 10 variables were used in the analysis (Table 2). They are in order of entry into the stepwise analysis: **ATT**, **TT**, **TSL**, **NS**, **MJS**, **ST**, **CLW**. **NS**, **ATT**, and **MJS** are most heavily load-



Text-figure 5.—Cluster analysis of all colonies of *Stephanocoenia* in the NMB collections. Dendrogram based on distances calculated using the average linkage method of the SAS CLUSTER procedure. Each terminal branch represents one colony. Colonies are labelled using NMB catalog numbers followed by either **S** or **D**. **S** = colonies later identified as *S. spongiformis*; **D** = colonies later identified as *S. duncani*. The cluster analysis was performed on principal component scores computed for all colonies in the NMB and modern collections. Clusters used initially in grouping specimens into species are indicated by double vertical lines.

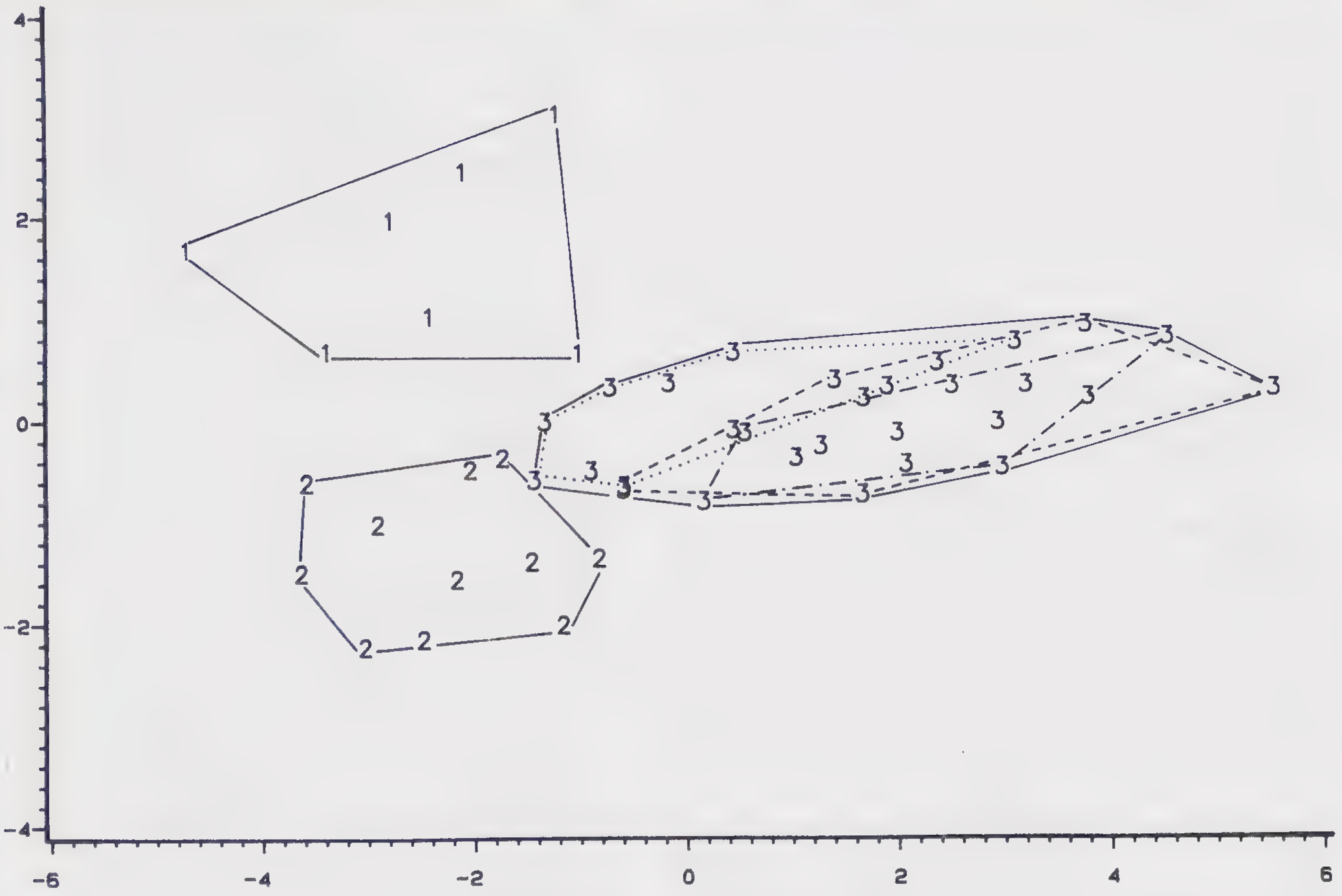
ed on the first function; and **ATT** and, to a lesser degree, **CLW** are most strongly correlated with it. This result suggests that thickness of such structures as the inner wall and the columella are most important in distinguishing the fossil from the modern *Stephanocoenia*. **NS**, **MJS**, and **TT** are most heavily loaded on the second function; and **TT** is most strongly correlated. This result suggests that the spacing between the corallites and the development of the intercostal area are most important in distinguishing the two fossil species.

In summary, three overlapping clusters (two fossil and one modern) exist, and seven of the measured characters are important in making the distinction. The greatest difference between the fossil and modern clusters occurs in the thickness of the inner wall and columella. The most overlap occurs between the cluster representing the modern species and that representing the new fossil species, *S. duncani*. The two fossil species are distinguished by corallite spacing and the development of the exothecal intercostal area. Thus, *S. spongiformis* appears more subcerioid, whereas *S. duncani* appears more cerioid.

Intraspecific Variation

Because of the overlap noted between species in the previous section, variation within species has been studied in more detail at two levels to determine if the clusters could represent true species. Variation was studied first within colonies and second between populations.

Variation within the fossil colonies was studied to determine if variability within colonies could be used to estimate variation within clusters. Study of such variation yielded two important results: (1) significant overlap exists between colonies within each cluster and the magnitude of this overlap appears far greater than the overlap between the two clusters (Text-fig. 8); and (2) despite the high magnitude of colony overlap, results of nested multivariate analysis of variance reveal a strong colony effect indicating that colonies within each cluster are significantly different. The overall mag-



Text-figure 6.—Canonical discriminant analysis between species of all *Stephanocoenia* in the NMB and modern collections. Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the three species groups defined by the statistical analyses. The points represent means for each colony. 1 = fossil NMB *S. spongiformis*, 2 = fossil NMB *S. duncani*, 3 = modern *S. intersepta*. In *S. intersepta*, dotted lines surround the lagoon population, dashed lines surround the reef population, and dotted/dashed lines surround the sand channel population.

Table 3.—Canonical discriminant analysis of three populations of modern *Stephanocoenia intersepta*. Total-sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The canonical variables are labelled CV1–2. Abbreviations for characters are explained in Table 1.

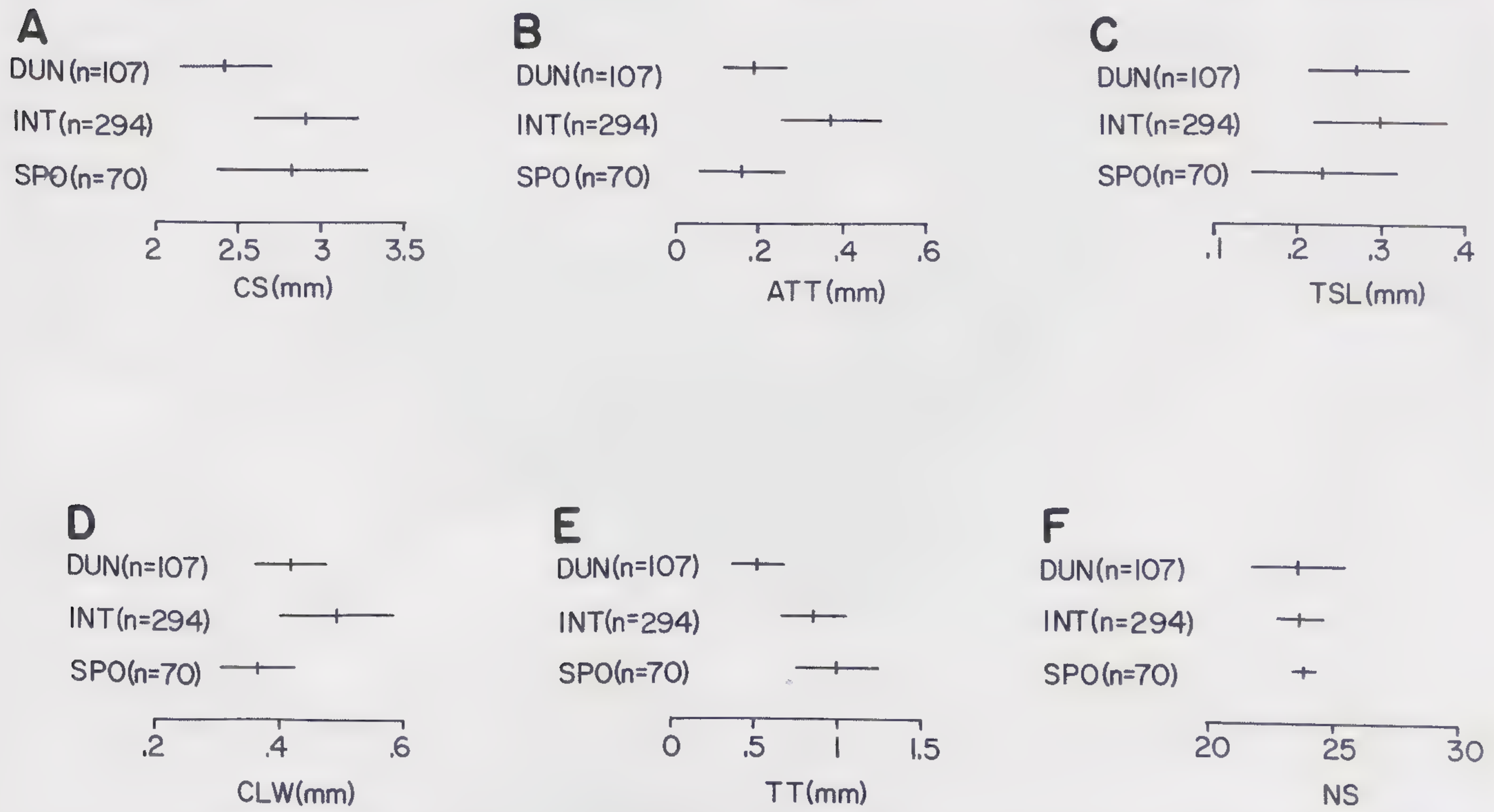
original variable	CV1		CV2	
	COR	SCC	COR	SCC
CD	.002	not used	.214	not used
CS	.080	−0.75*	.189	−0.04
CLW	.495*	0.36	.562*	1.03*
TSL	.032	not used	.118	not used
TT	.073	not used	.065	not used
ATT	.625*	0.67*	.282	0.24
ST	.556*	0.47	.023	−0.66
NAC	.150	not used	.259	not used
NS	−.363	−0.54	.480	0.79
MJS	−.373	not used	.360	not used

* Most important variables.

nitude of variation in the two clusters appeared equal, and results of Box's tests (Miller, 1968) show that variation within colonies of each cluster appeared equal. Thus, because of differences between colonies within clusters, variation within colonies cannot be used directly to estimate variation within clusters. The amount of overlap between colonies differs in degree from that between clusters.

Variation between populations of modern *S. intersepta* was studied to determine if differences between populations were similar to differences between species. To do this, first, canonical discriminant analysis was performed for the three populations of the modern species (Table 3, Text-fig. 9). In this analysis, 76.7 percent of all colony means were correctly classified. This value is more than 10 percent lower than the percentage calculated in the analysis discriminating between species clusters. The most significant overlap occurred between the nearby, environmentally-similar reef and sand channel localities. When the values for these two populations were pooled, the percentage of correctly-classified colonies was raised to 90 percent, a value similar to that for the analysis between species clusters. Thus, it can be concluded that the modern populations overlap to the same degree as the species clusters. However, it must be noted that the actual difference between the species clusters is far greater than that between modern populations (Text-fig. 6).

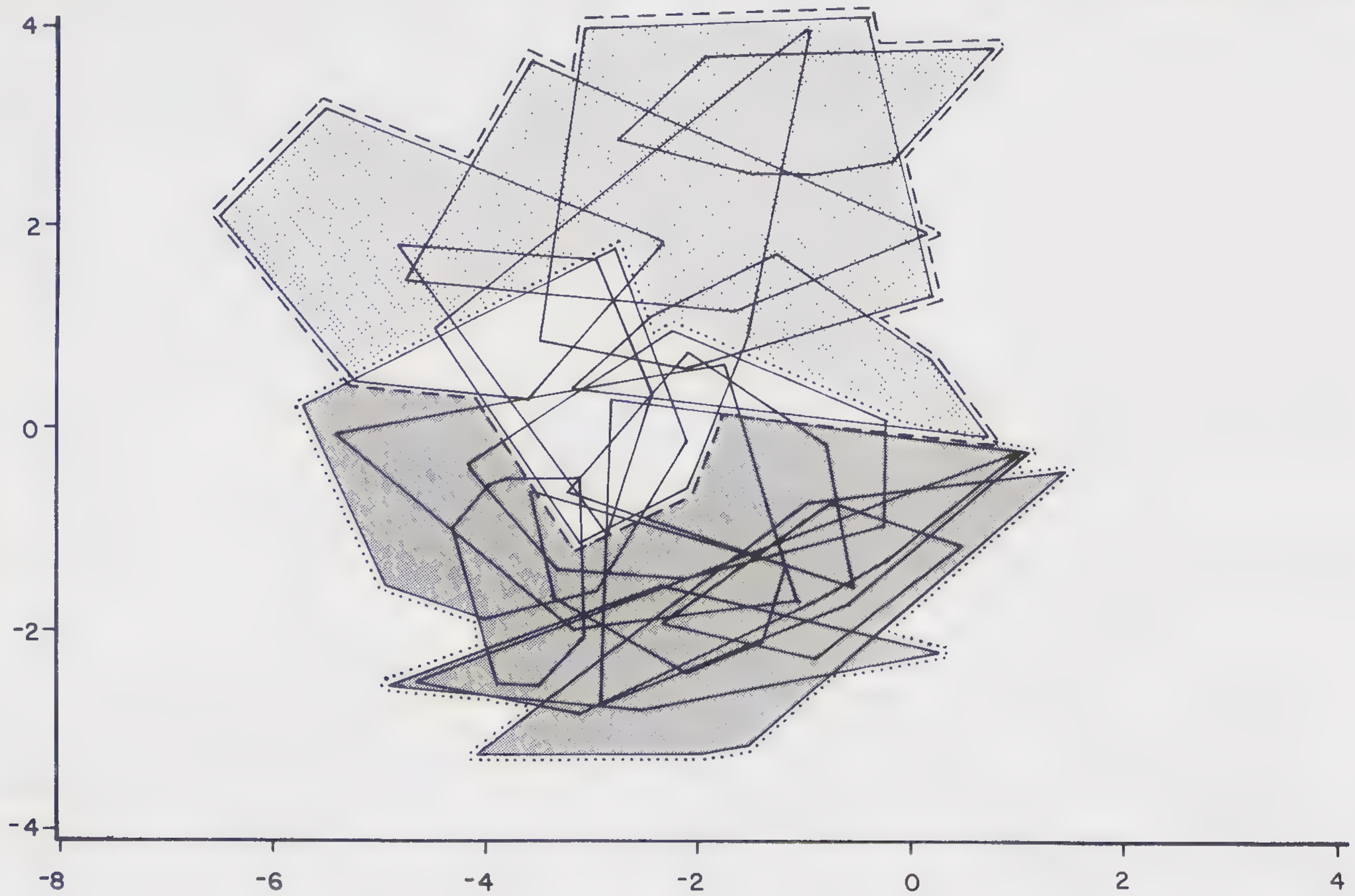
Two discriminant functions were calculated in the analysis for the three modern populations, the first accounting for 78.78 percent of the variation and the second for 21.22 percent. The first function primarily distinguishes the lagoon group from the reef and sand channel groups, whereas the second function distin-



Text-figure 7.—Means and standard deviations for six characters in the two NMB and one modern species. The midpoint of each horizontal line represents the mean, and the length of the line on either side of the midpoint is one standard deviation. Analysis of variance (or Welch's statistic when variances are unequal) shows that the species are significantly different in every case except **NS**. **SPO** = species 1, fossil NMB *S. spongiformis*; **DUN** = species 2, fossil NMB *S. duncani*; **INT** = species 3, modern *S. intersepta*. **n** = number of corallites measured. (A) corallite spacing, **CS**, (B) inner wall thickness, **ATT**, (C) tertiary septum length, **TSL**, (D) columella width, **CLW**, (E) total theca width, **TT**, (F) total number of septa, **NS**.

guishes the sand channel group from the reef and lagoon groups. Five of the 10 variables were used in the analysis (Table 3). They are, in order of entry into the analysis: **ATT**, **NS**, **CLW**, **CS**, **ST**. **CS**, **ATT**, and **NS** are most heavily loaded on the first function; and **ATT** and **ST** are most strongly correlated with it. This result suggests that the thickness of the inner wall and the septa are most important in distinguishing the lagoon population from the two forereef populations. **CLW**, **NS**, and **ST** were most heavily loaded on the second function; and **CLW** and **ST** are most strongly correlated with it. This result suggests that thickness of the columella and the septa are most important in distinguishing between the two forereef populations (Pl. 1).

To determine if these two new discriminant functions are related to the original two functions distinguishing the species clusters, Spearman's rank correlation coefficients were calculated between pairwise combinations of the four functions using all fossil and modern colony means. The results show a very high correlation between the first canonical variable of the between-species analysis and the first canonical variable of the between-population analysis ($r_S = 0.97469$; $p = 0.0001$). In other words, the same variables that distinguish the fossil species from the modern species also distinguish the modern lagoon population from the two modern forereef populations. This result further supports the hypothesis that *S. duncani* and *S. intersepta* represent parts of a morphologic continuum formed by one continuous species. However, as a complicating factor, the lagoon population lies intermediate between *S. duncani* and the two forereef populations of *S. intersepta* (Text-fig. 6). Of the three habitats studied, the lagoon represents a high stress, environmental extreme, which is especially muddy with low circulation. Therefore, it should be most similar in environment to the lowest portion of the Cibao Valley sections, assuming the sequence deepens upward as interpreted by Saunders, Jung, and Biju-Duval (1986), and not to the uppermost part of the sequence as shown in Text-figure 6. Furthermore, colonies from the lowest portion of the Cibao Valley sections appear to have a

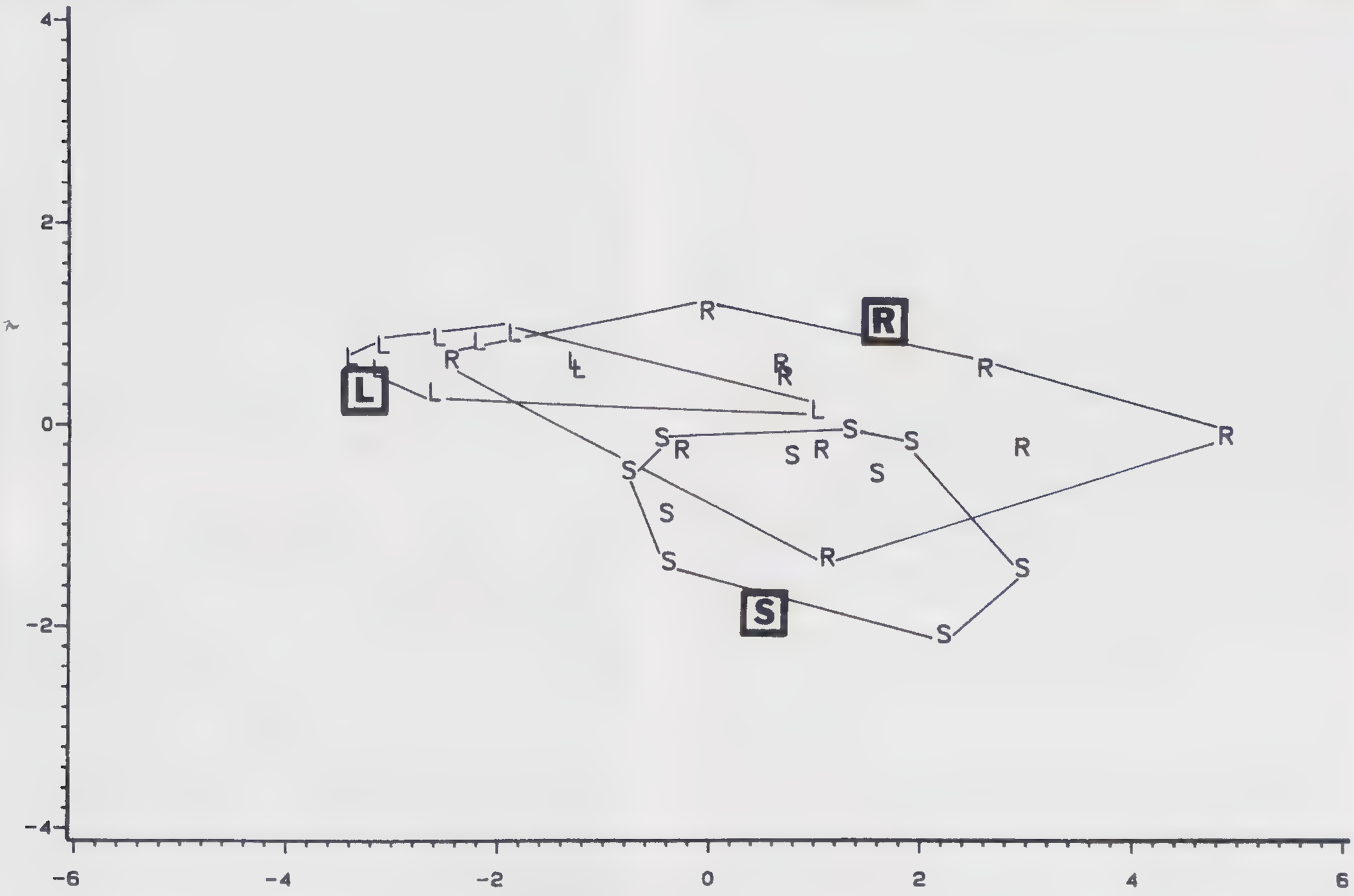


Text-figure 8.—Intraspecific variation in the two fossil NMB species for canonical variables 1 and 2 of the canonical discriminant analysis between species of *Stephanocoenia* (Text-fig. 7, Table 2). Each smaller polygon surrounds the variation observed within one colony. The total area covered by polygons of *S. spongiformis* is lightly shaded and outlined with a dashed line. The total area covered by polygons of *S. duncani* is darkly-shaded and outlined with a dotted line. The area of overlap between species is left unshaded. Considerable overlap is seen between colonies within species and, to a lesser extent, between species.

skeletal morphology more extreme than that found in even the most extreme, high-stress modern environment (*i.e.,* the lagoon). Consequently, the postulated morphologic continuum cannot be explained as a response to change in environment alone.

In summary, study of intraspecific variation reconfirms that the species in the genus *Stephanocoenia* do not form discrete clusters composed of uniform entities. Variation within species is large, its magnitude cannot be estimated by variation within colonies, and colonies within species differ significantly. Overlap between the three populations of the modern species occurs to the same degree as overlap between the three species, although overall variation between populations of the modern species is significantly lower in magnitude than variation between species. Two species (one fossil, one Recent) appear to form a morphologic continuum, suggesting that they represent chronospecies within one lineage. This continuum cannot be explained as an ecophenotypic response to change in environment alone.

Comparison of these evolutionary patterns in *Stephanocoenia* with those exhibited by species of the family Poritidae from the same sections shows similarities and differences between evolutionary patterns in the two groups and between patterns of intraspecific variation in the two groups. *S. spongiformis* has a short duration and is morphologically stable as is common among the poritid species. However, it was not as abundant or widely distributed as were many poritids. In fact, *Stephanocoenia* itself appears restricted to the Caribbean throughout the Neogene. In contrast to *S. spongiformis, S. duncani* exhibits gradual directional evolution. Like the poritids, *S. spongiformis* becomes extinct during the mid- to late Pliocene or early Pleistocene when a mass extinction occurred among many tropical marine invertebrates (Stanley, 1984). *S. duncani* may have continued its gradual evolution through the extinction interval. Unlike the poritids, *Stephanocoenia* does not experience a radiation of new taxa after the late Neogene to early Quaternary extinction. Both the poritids and *Stephanocoenia* exhibit large



Text-figure 9.—Canonical discriminant analysis between populations of modern *Stephanocoenia intersepta* from three different reef habitats near Discovery Bay, Jamaica. Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies within each population. The points represent colony means. **L** = lagoon population, **R** = forereef coral thicket population, **S** = forereef sand channel population.

amounts of intraspecific variability, which is more directly related to environment in *Stephanocoenia*. Although more extensive among the poritids, overlap between species occurs in both groups.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Using the classification system of Wells (1956), the family Astrocoeniidae Koby, 1890 is represented by only one genus in the collection of Saunders, Jung, and Biju-Duval (1986). The family itself is described as colonial, having extratentacular budding, a phaceloid to cerioid colony form, a septothecal wall structure, beaded septal margins, and a styliform columella (if any). The septa are composed of few, simple trabeculae. No attempt will be made to formally describe the family herein, since considerable doubt has been expressed as to whether the family represents a true monophyletic group and it therefore is much in need of revision (see Veron and Pichon, 1976). Of the 13 genera that Wells (1956) included in the family, seven are exclusively Mesozoic, three occur in Eocene to Miocene deposits (*Platycoenia* Vaughan, 1900, *Stylocoenia* Milne-Edwards and Haime, 1848a, and *Astrocoenia* Milne-Edwards and Haime, 1848a), two range in distribution from Mesozoic to Recent (*Stephanocoenia* and ?*Actinastraea* d'Orbigny, 1849), and one (*Stylocoeniella* Yabe and Sugiyama, 1935) extends from Eocene to Recent. Only three (*Astrocoenia, Stephanocoenia,* and *Stylocoenia*), however, are commonly reported in the Neogene of the Caribbean (Vaughan, 1919), and three (*Stylocoenia,* ?*Actinastraea,* and ?*Platycoenia*) in the Neogene of the Mediterranean (Chevalier, 1961). Thus, both *Astrocoenia* and *Stephanocoenia* were restricted to the Caribbean during the Neogene, even though the distributions of both genera extended across the Atlantic during the Oligocene (Vaughan, 1919; Frost, 1981). An interesting question involving these taxa, from a Caribbean perspective, is why *Astrocoenia* and *Stylocoenia* do not occur in the Dominican Republic Neogene. The answer cannot be resolved without more rigorous study of the common Neogene species involved [*A. guantanamensis* Vaughan, 1919 (= *A. decaturensis* Vaughan, 1919 = *A. portoricensis* Vaughan, 1919); *A. meinzeri* Vaughan, 1919; and *S. pumpellyi* (Vaughan, 1900)].

The formal systematic descriptions that follow are based strictly on the results of the statistical analyses presented in the previous section. As in Foster (1986), the term "diagnosis" is used only to describe higher categories such as genera, whereas the term "description" is reserved for complete descriptions of species, which, as described in the previous section, herein represent merely morphologic clusters of specimens. The terminology used in the "Description" sections is defined and described in the previous section entitled "Characters". It follows the usage of Vaughan and Wells (1943) and Wells (1956). The abbreviations used for measurements are explained in Table 1 and are identical to those used in the statistical analyses.

The "Material" sections give an approximate estimate of the amount of material in the collection of Saunders, Jung, and Biju-Duval (1986) and the number of specimens in this collection that were statistically analyzed. Unless otherwise indicated, the locality numbers belong to the Naturhistorisches Museum Basel (NMB) and material is deposited at the NMB. Assignment of formation names to individual localities is based on Saunders, Jung, and Biju-Duval (1986) (especially text-figs. 4, 6, 15, 16), except along Río Mao where formation names are used as listed by Maury (1919). Catalogue numbers have been assigned to all figured and measured material. A unique number was given to each colony.

The "Remarks" sections explain synonymies and additional museum material used to estimate distribution patterns. Separate sections entitled "Variability" describe the variation within each cluster. Sections entitled "Occurrence" give detailed geographic and stratigraphic information within the studied areas of the Dominican Republic, whereas those entitled "Distribution" give general information on all known occurrences throughout the world. Ages for Caribbean localities mentioned outside the Dominican Republic are based on the following sources: Jamaica, Zans *et al.* (1963); Trinidad, J. B. Saunders (oral commun., 1985).

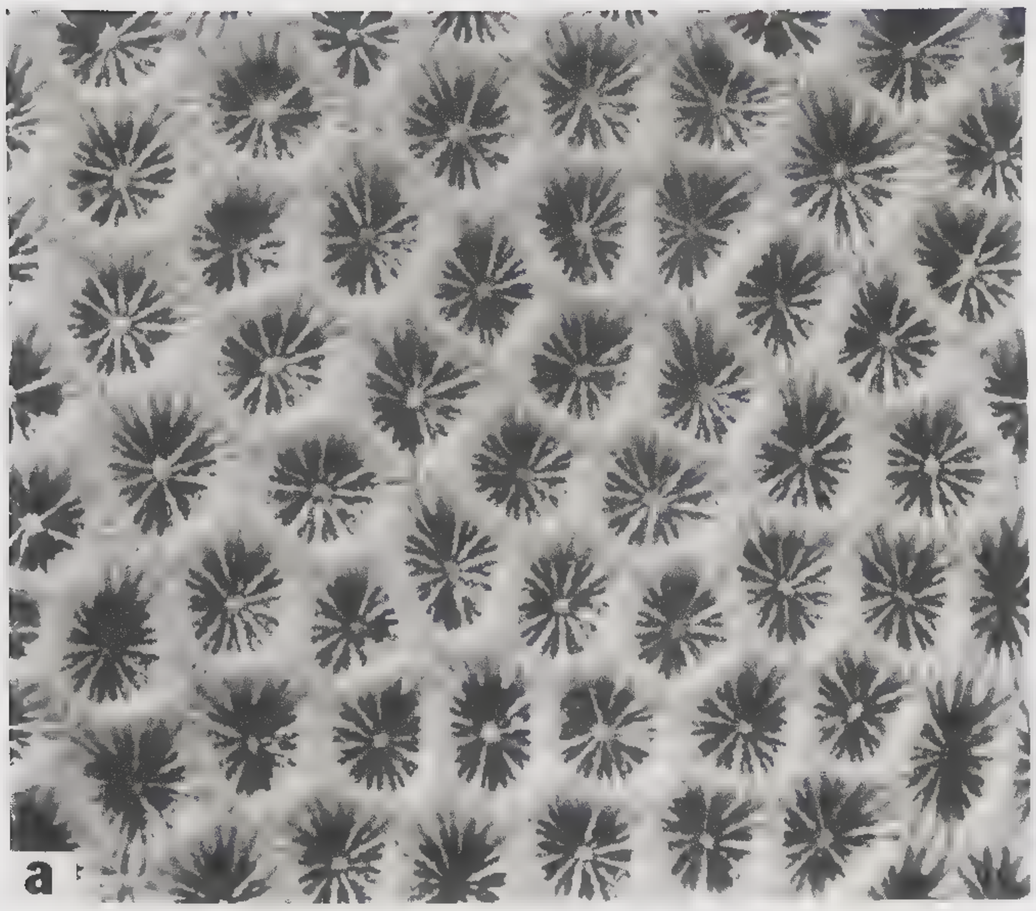
Genus **STEPHANOCOENIA** Milne-Edwards and Haime, 1848

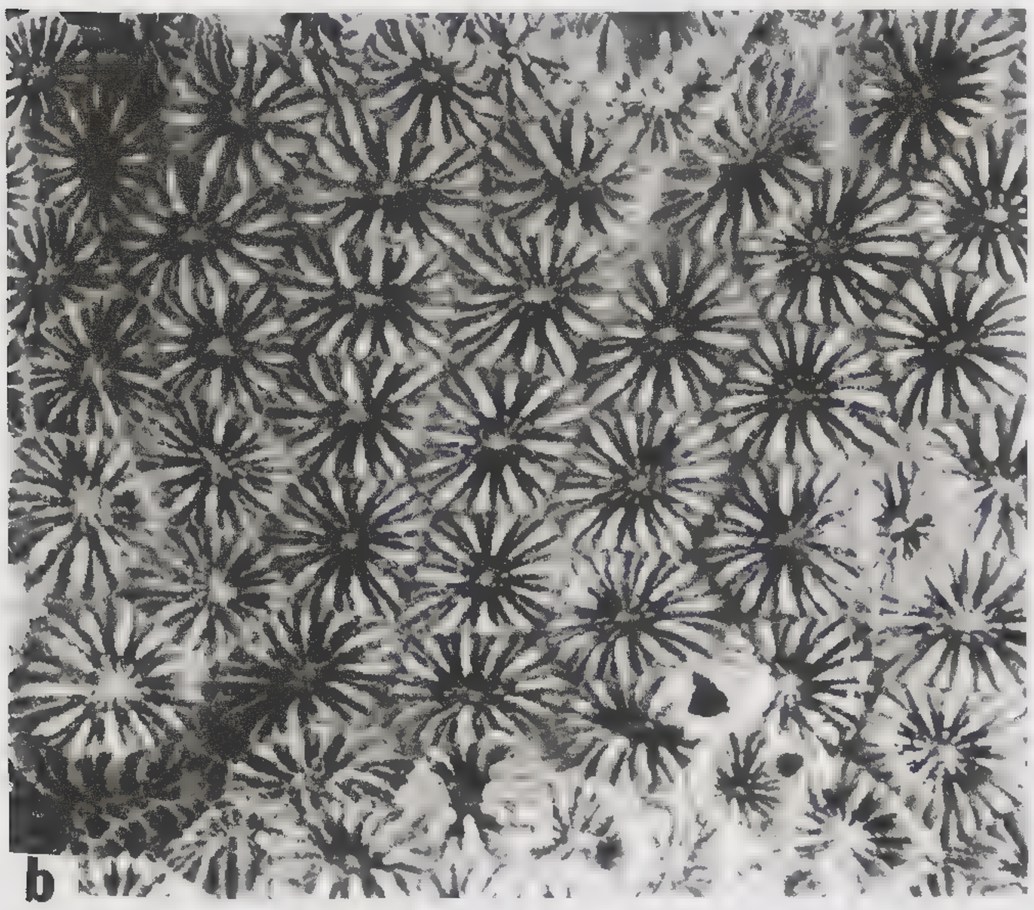
Stephanocoenia Milne-Edwards and Haime, 1848a, p. 469.
Antillastraea Duncan, 1884, p. 108.

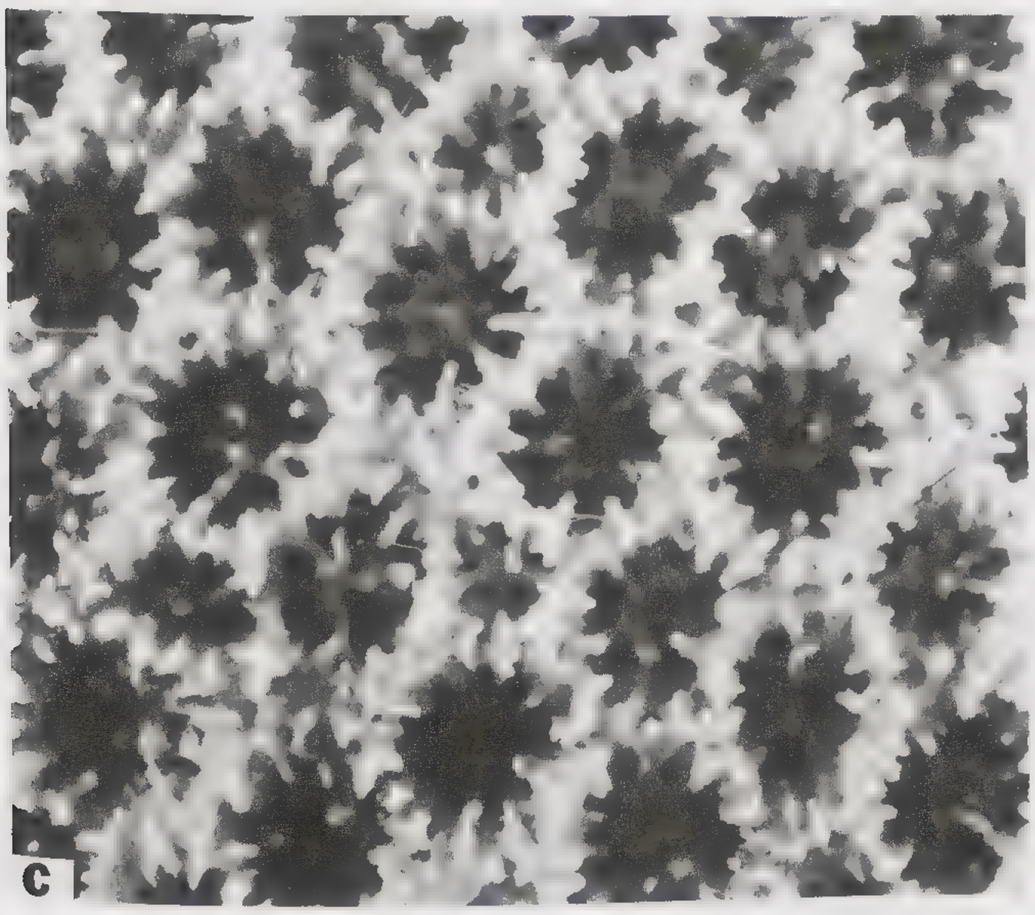
Type species.—*Astrea intersepta* Lamarck, 1816, p. 266.

Diagnosis.—Colonies massive, plocoid to subcerioid. Corallites budded extratentacularly, 1–3 mm in diameter. Septa usually 24 in number arranged in three cycles (six primaries, six secondaries, and 12 tertiaries); composed of six to eight trabeculae that form minute denticles along the septal margins. Costae short, equal. One crown of 12 pali (or a multiple of six) before first two septal cycles. Walls septothecal to parathecal. Columella styliform. Endothecal and exothecal dissepiments tabular with uniform spacing.

Remarks.—Milne-Edwards and Haime (1848a, p. 469) described the genus *Stephanocoenia* citing "*Astrea intersepta* Lamarck" as the type species. Lamarck (1816, p. 266) described the species *Astrea intersepta* citing "*An madrep. intersepta ?* Esper, suppl. I, t. 79" as the only reference. Lamarck's specimen is figured







here in Text-figure 10a. According to M. E. Tollitt (written commun., 1984) and R. V. Melville (written commun., 1984) of the International Commission on Zoological Nomenclature, the question mark in Lamarck's citation indicates that "he was not satisfied that the two species were identical" and that "Lamarck was clearly describing a different species from Esper's" (letter dated 8 June, 1984, from R. V. Melville to the author).

If Lamarck (1816) is interpreted not to have been describing a new species but citing Esper (1795) as the author of *intersepta,* multiple nomenclatural complications would ensue, since re-examination of Esper's material shows that Esper's (1795, vol. 1, p. 99, pl. 79) *Madrepora intersepta* is clearly a member of the genus *Alveopora* Blainville, 1830 of the family Poritidae in the classification system of Vaughan and Wells (1943) and Wells (1956). Esper's specimen is figured here in Text-figure 10c. Accepting Esper as the author of the Lamarck *intersepta* would thus relegate Milne-Edwards and Haime's generic name "*Stephanocoenia*" to a junior synonym of *Alveopora,* leaving the name *Antillastraea* Duncan, 1884 as the next chronologically valid generic name for Lamarck's coral.

Assuming that Lamarck's *intersepta* was not the same as Esper's *intersepta,* many Caribbean scleractinian workers (*e.g.,* Smith, 1948; Squires, 1958; Almy and Carrión-Torres, 1963; Laborel, 1969; Cairns, 1982) have recently assigned the name *Stephanocoenia michelini* Milne-Edwards and Haime, 1848b (vol. 10, p. 301, originally spelled "*michelinii*" in error) to Lamarck's species, since *michelini* has been usually synonymized with Lamarck's *intersepta* [after Gregory, 1895, pp. 276–277] and it is chronologically the next specific name that would apply. The holotype of *michelini* is figured here in Text-figure 10b. The present study of this problem, however, indicates that the species should be referred to as *Stephanocoenia intersepta* (Lamarck, 1816) and not as *Stephanocoenia michelini* Milne-Edwards and Haime, 1848b. This

Text-figure 10.—Photographs of the colony surfaces of three holotypes important in the nomenclatural problem involving *Stephanocoenia intersepta* (Lamarck, 1816). **A**. *Stephanocoenia intersepta* (Lamarck, 1816), Lamarck collection, MNHNP, "les mers Australes", Recent, ×5 (photo by M. Serrette, MNHNP). This specimen was used by Lamarck (1816) to describe the species *Astrea intersepta.* It was later used by Milne-Edwards and Haime (1848a) to describe the genus *Stephanocoenia.* **B**. *Stephanocoenia michelini* Milne-Edwards and Haime, 1848b, Michelin collection, MNHNP, locality unknown, Recent, ×5 (photo by M. Serrette, MNHNP). This species has been synonymized with *S. intersepta,* since Gregory (1895). Because of the nomenclatural problem involving the name *intersepta,* several authors have used the name *michelini* to refer to the species. **C**. *Alveopora intersepta* (Esper, 1795), Esper Collection 68, NMS, East Indian Ocean, Recent, ×9.6 (photo by G. Scheer). This specimen was Esper's (1795) original specimen of *intersepta,* which has recently been assigned to the genus *Alveopora.*

practice follows that of the recent book by Zlatarski and Estalella (1982), although these authors were apparently unaware of the problem with Esper's specimen.

The genus *Stephanocoenia* occurs today only in the Caribbean and is represented by only one species, *Stephanocoenia intersepta* (Lamarck, 1816). Its modern geographic distribution ranges from Bermuda throughout the Caribbean as far south as Brazil. Ecologically, *Stephanocoenia* is common in many reef habitats extending from the lagoon across the reef crest (1 m depth) to the deep forereef (greater than 95 m depth). Its optimal depth range is 3–50 m (Goreau and Wells, 1967).

Because various, poorly-preserved plocoid fossil corals have been assigned at some time to the genus *Stephanocoenia,* it is extremely difficult to determine its temporal distribution based on limited study of the literature. *Stephanocoenia* is clearly distinguished from other astrocoeniid and plocoid corals by: (1) its prominent pali, (2) its styliform columella, (3) its subcerioid growth form, and (4) its numerous septa usually arranged in cycles of six. Based on these criteria, *Stephanocoenia* has occurred in the Caribbean since the lower Cretaceous (Wells, 1932; Wells, 1933). However, it may have been extremely rare during the Paleogene, since it has only been described from the Eocene of Peru (Wells, 1941). Some doubt exists as to whether *Stephanocoenia* occurred in the European Cretaceous (Alloiteau, 1957, pp. 56–57), although it was common in the Mediterranean during the Paleogene (Frost, 1981). It is not known from the Mediterranean Neogene (Chevalier, 1961). *Stephanocoenia* has been common in the Caribbean from mid-Miocene to Recent (Vaughan, 1919; Frost, 1977).

A number of Tertiary coral species that were originally assigned to *Stephanocoenia* do not belong, including: *Stephanocoenia reussi* Duncan, 1867 (= *Hydnophora* Fischer, 1807), *Stephanocoenia tenuis* Duncan, 1863 (= *Goniopora* Blainville, 1830), *Stephanocoenia dendroidea* Milne-Edwards and Haime, 1860 (= *Madracis* Milne-Edwards and Haime, 1849), *Stephanocoenia fairbanksi* Vaughan, 1900 (= *Solenastrea* Milne-Edwards and Haime, 1848a), and *Stephanocoenia* ? *decaseptata* Weisbord, 1971 (= *Madracis*). Only two names have been proposed for true representatives of the genus in the Caribbean during the Neogene: *Stephanocoenia intersepta* (Lamarck, 1816) and *S. spongiformis* (Duncan, 1864). Gregory (1895) and Vaughan (1919) synonymized the two names.

Stephanocoenia spongiformis (Duncan, 1864)
Plate 2, figures 1–8; Plate 3, figures 1–6; Plate 4, figures 1–6; Text-figures 2, 3, 6, 7, 8

Plesiastraea spongiformis Duncan, 1864, p. 39, pl. 4, figs. 6a, 6b.

Description.—Colonies massive, hemispherical, small to intermediate in size (1.5–15 cm in length, 1.5–6.5 cm in height) with smooth outer surfaces. Growth bands well developed at regular 2–3 mm intervals. Epitheca reduced, with irregular growth ridges at less than 1 mm intervals. Calices circular in shape; small in size (1.3–2.3 mm in diameter) and shallow in depth (less than 1 mm); with wide spacing (0.5–1.5 mm between adjacent calices) giving the colony form a subcerioid appearance. Theca composed of a thin, well-defined, parathecal wall, circular in shape, surrounding each corallite. A second, equally well-defined polygonal wall (that may form a prominent ridge) demarcates the junctions between adjacent corallites. The two walls are separated by void space which is regularly subdivided by costae of equal thickness. These costae extend completely from the outer margin of each septum to the second wall. Septa approximately 24 in number, composed of six trabeculae (not including pali) that form fine surface denticles. Primary and secondary septa of equal length extending completely to the columella. Tertiary septa free, one-third to one-half the length of the first two cycles. Pali reduced, 12 in number, formed by thickening of two to three trabeculae at the inner margins of the first two septal cycles. Columella forming a prominent style, 0.2–0.5 mm in diameter. Endothecal dissepiments thin, at 0.4 mm intervals. Exothecal dissepiments moderately thick (0.04 mm) at 0.3 mm intervals. Exothecal dissepiments moderately thick (0.04 mm) at 0.3 mm intervals, forming uniform, approximately square cellular voids.

Holotype.—BM(NH) R28756 (figured here: Pl. 2, figs. 7, 8).

Measurements of the holotype.—Colony length, 5.10 cm; colony width, 4.96 cm; colony height, 5.75 cm. The holotype for this species has not been thin-sectioned; therefore, the following characters were measured on the colony surface and are not as accurate as the thin-section measurements given above in the species description. They cannot be directly compared with the thin-section measurements given in Text-figure 7 and the Appendix. Each value represents the mean of 10 corallites. **CD**, 2.6; **TT**, 1.0; **NS**, 24.2; **CLW**, 0.7; **ATT**, 0.13; **ST**, 0.12; **TSL**, 0.4.

Type locality.—"silt of the Sandstone plain" of Heneken (1853), Dominican Republic, Neogene.

Material.—Thirty-two colonies from 16 localities. Seven colonies thin-sectioned and measured.

Remarks.—Duncan (1864) recognized two species which belong to *Stephanocoenia* in the Heneken collection of fossil corals from the "silt of the Sandstone plain" of the Dominican Republic: "*Stephanocoenia intersepta,* var., Edwards & Haime" [p. 27, BM(NH) R28811] and "*Plesiastrea spongiformis,* spec. nov." [p. 39, BM(NH) R28756]. Re-examination of these two

specimens shows the first to belong to *S. duncani* as defined herein and the second to belong to *S. spongiformis* as defined herein. Duncan (1884) later designated *spongiformis* as the type species of his new genus *Antillastraea.* Gregory (1895) and Vaughan (1919) synonymized the species *spongiformis* with *S. intersepta* and consequently the genus *Antillastrea* with *Stephanocoenia,* because they could not recognize consistent distinctive characteristics in the material at the BM(NH), which Duncan labelled "*spongiformis*". Nevertheless, Duncan's holotype of *spongiformis* clearly lies within the range of one of the two fossil species defined statistically in the present study. Therefore, Duncan's name is reinstated.

Variability.—Variation within this species is consistently high as in *S. duncani.* Colonies differ widely from one another (Text-fig. 8); however, the variation does not appear directly related to environment. No directional morphologic trends were observed up the studied sequence. From colony top to bottom, corallite diameter increases, total theca width increases, skeletal structures thicken, and pali become better developed.

Comparison.—*S. spongiformis* is distinguished by its well-developed, porous exothecal intercostal area and by its thinner skeletal structures. It differs statistically from the fossil species *S. duncani* by having wider corallite spacing, a smaller columella, shorter tertiary septa, a wider intercostal area, and a thinner inner wall. It differs statistically from the modern species *S. intersepta* by having a smaller corallite diameter, a thinner columella, shorter tertiary septa, a wider intercostal area, a thinner inner wall, and thinner septa (Text-fig. 7). Its pali are elongate and poorly developed, although better developed than in *S. duncani*; and its colonies are small in size.

Occurrence.—Río Cana: Gurabo Formation (locs. NMB 16818, 16865) and Mao Formation (loc. NMB 16884).

Río Gurabo: Gurabo Formation (locs. NMB 15846, 15847, 15850, 15853, 15855, 15858, 15859, 16811, 16883, 16934) and Mao Formation (locs. NMB 15822, 15830, 15834).

Distribution.—This species is not known to occur outside the lower to middle Pliocene of the Dominican Republic.

Stephanocoenia duncani, new species
Plate 5, figures 1–6; Plate 6, figures 1–6; Plate 7, figures 1–6; Text-figures 2, 3, 6, 7, 8

Etymology of the name.—After P. M. Duncan, who first recognized the species as a variety.

Description.—Colonies massive, hemispherical, sometimes moderately large in size (6–30 cm in length, 3–14 cm in height) with smooth outer surfaces. Growth bands well developed at regular 3–5 mm intervals. Epitheca reduced, with irregular growth ridges at 1 mm intervals. Calices polygonal in shape; small in size (1–2.4 mm in diameter) and shallow in depth (approximately 1 mm); with narrow spacing (0.2–1 mm between adjacent corallites) giving the colony form a cerioid appearance. Theca composed of a thick septothecal wall separated from theca of adjacent corallites by little or no void space. A thin, poorly-developed second wall may form between thecae of adjacent corallites. Septa 22 to 24 in number, composed of six trabeculae that form minute surface denticles. Primary and secondary septa of equal length extending completely to the columella. Tertiary septa free, one-half to three-quarters the length of the first two cycles. Pali weak, 12 in number, formed by thickening of two trabeculae on the inner margins of the first two septal cycles. Columella forming a prominent style, 0.3–0.6 mm in diameter. Endothecal dissepiments thin and at 0.4 mm intervals. Exothecal dissepiments thick (0.2 mm), at 0.5 mm intervals. Exothecal dissepiments forming elongate voids, separated by thin, irregular vertical trabeculae.

Holotype.—NMB D5766 (figured here: Pl. 5, figs. 2, 4–6; Pl. 7, figs. 1, 2, 5).

Measurements of the holotype.—Colony length, 23.8 cm; colony width, 18.7 cm; colony height, 12.8 cm. The following measurements were made on thin-sections. Each value represents the mean of 10 corallites. **CD**, 2.06; **CS**, 2.48; **CLW**, 0.48; **TSL**, 0.26; **TT**, 0.51; **ATT**, 0.229; **ST**, 0.074; **NAC**, 6.4; **NS**, 24.0; **MJS**; 12.0.

Type locality.—Locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Lower Pliocene (Saunders, Jung, and Biju-Duval, 1986, text-fig. 15).

Paratypes.—NMB D5765, D5768, D5769, D5771, D5868, D5870, D5871 (figured here: Pl. 5, figs. 1, 3; Pl. 6, figs. 1–6; Pl. 7, figs. 3, 4). BM(NH) R28811, one of Duncan's (1864, p. 27) specimens of *S. intersepta,* var.

Material.—Twenty-four colonies from 11 localities. Ten colonies thin-sectioned and measured.

Remarks.—As explained in the Remarks section of the previous species, specimens of this species in the BM(NH) Heneken collection from the "silt of the Sandstone plain" of the Dominican Republic were labelled "*Stephanocoenia intersepta,* var." by Duncan (1864, p. 27). Vaughan (1919) also placed this species within *S. intersepta.* One of Duncan's specimens [BM(NH) R28811] is designated as a paratype.

Variability.—Variation within this species is high, as in *S. spongiformis*; however, variation between colonies may not be as extensive as in *S. spongiformis* (Text-fig. 8). An increase in the thickness of skeletal

structures such as the inner wall and the columella up the studied stratigraphic sequence have been detected. This increase is interpreted as evolutionary, although environmental factors could be at least partially responsible. Variation within colonies is equally as high as that observed in *S. spongiformis*. From colony top to bottom, corallite diameter increases, wall thickness increases, and various skeletal structures appear more heavily calcified.

Comparison.—*S. duncani* is distinguished primarily by its poorly-developed, denser intercostal area giving the colony form a cerioid appearance; by its especially weak pali; by its predominantly septothecal wall structure; and by its thicker skeletal structures. It differs statistically from the fossil species *spongiformis* by having closer corallite spacing, a thicker columella, shorter tertiary septa, a narrower intercostal area, and a thicker inner wall. It differs statistically from the modern species *intersepta* by having a smaller corallite diameter, closer corallite spacing, a thinner columella, shorter tertiary septa, a narrower intercostal area, a thinner inner wall, and thinner septa. It sometimes forms large colonies.

Occurrence.—Río Cana: Gurabo Formation (locs. NMB 16815, 16817, 16818, 16819, 16881) and Mao Formation (loc. NMB 16874). Río Gurabo: Gurabo Formation (locs. NMB 15855, 16933, 16934). Río Mao: ?Gurabo Formation (loc. NMB 16911). Río Yaque del Norte: Baitoa Formation (loc. NMB 16943).

Distribution.—*Stephanocoenia duncani* ranges in age from middle Miocene to middle Pliocene and is rare in the southern and central Caribbean. Outside the studied sequence in the Dominican Republic, it occurs in the following strata: ?Miocene.—Rio Yaque del Sur section of the Dominican Republic, and St. Croix, Trinidad; Pliocene.—Bowden Formation of Jamaica.

Appendix. Means (±1 standard deviation) of all corallite characters in the two fossil species of *Stephanocoenia* and in three populations of modern *Stephanocoenia intersepta*. "N" refers to the number of corallites measured. Ten corallites were measured in each colony. See Table 1 for explanations of character abbreviations.

Variable	*S. spongiformis* N = 70	*S. duncani* N = 110	*S. intersepta* N = 100 (lagoon)	*S. intersepta* N = 100 (forereef)	*S. intersepta* N = 100 (sand channel)
CD	1.91 (±.21)	1.97 (±.28)	2.01 (±.25)	2.08 (±.24)	2.10 (±.19)
CS*	2.82 (±.46)	2.42 (±.28)	2.86 (±.34)	2.94 (±.35)	2.90 (±.26)
CLW*	.365 (±.062)	.418 (±.058)	.434 (±0.64)	.536 (±.098)	.508 (±.081)
TSL*	.230 (±.088)	.268 (±.061)	.300 (±.091)	.295 (±.079)	.293 (±.072)
TT*	.990 (±.251)	.512 (±.164)	.839 (±.248)	.866 (±.174)	.842 (±.163)
ATT*	.156 (±.104)	.188 (±.078)	.296 (±.129)	.406 (±.100)	.407 (±.093)
ST	.071 (±.017)	.076 (±.019)	.076 (±.014)	.090 (±.018)	.094 (±.016)
NAC	6.48 (±.68)	6.36 (±.77)	6.41 (±.88)	6.35 (±.70)	6.44 (±.80)
NS*	23.86 (±.49)	23.59 (±1.90)	23.91 (±.62)	23.79 (±1.04)	23.37 (±1.19)
MJS	11.91 (±.28)	11.79 (±.95)	11.94 (±.34)	11.83 (±.69)	11.53 (±.95)

* Characters whose means and standard deviations are diagrammed in Text-figure 7.

NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC

5. The Suborders Caryophylliina and Dendrophylliina (Anthozoa: Scleractinia)

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ABSTRACT

The 20 species of Neogene Scleractinia in the suborders Caryophylliina and Dendrophylliina known from the Dominican Republic are revised and illustrated. This research was based on 1590 specimens obtained primarily from the collections of the Naturhistorisches Museum, Basel, Switzerland; National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; and Tulane University, New Orleans, LA, U.S.A. Eight new records are reported for the Neogene of the Dominican Republic, including four new species: *Antillocyathus alatus, Trochocyathus chevalieri, T. duncani,* and *Paracyathus sinuosus.* Special attention is given to the genus *Asterosmilia,* since half (five) of the known species in this genus occur in the Dominican Republic.

Most species described herein are assumed to constitute a deep-water fauna by analogy to depth ranges of the same or similar species known from the Recent. Certain localities and parts of formations are inferred to represent deep-water (>200 m) facies. These inferences may aid in the paleoecological interpretation of other fossils collected from these areas.

RESUMEN

Las veinte especies de Scleractinia Neogene de los subórdenes Caryophylliina y Dendrophylliina que se conocen de la República Dominicana, son revisadas e ilustradas. Esta investigación fue hecha sobre una base de 1590 especímenes obtenidos, primariamente, de las colecciones del Naturhistorisches Museum, Basel, Suiza; el Museo Nacional de Historia Natural, Smithsonian Institution, Washington, DC, EEUU; y Tulane University, New Orleans, LA, EEUU. Se registran ocho localidades nuevas para las especies de Neogene de la República Dominicana, incluyendo en las mismas cuatro especies nuevas: *Antillocyathus alatus, Trochocyathus chevalieri, T. duncani,* y *Paracyathus sinuosus.* Se brinda atención especial al género *Asterosmilia,* puesto que la mitad (cinco) de las especies conocidas, del mismo, se encuentran en la República Dominicana.

Se presume que la mayoría de las especies descriptas en esta obra constituyen una fauna de agua profunda por analogía a los rangos de profundidad de las mismas o especies similares conocidas de la época Reciente. Se infiere que ciertas localidades y partes de las formaciones representan las facies de agua profunda (>200 m). Estas inferencias pueden ayudar a la interpretación de otros fósiles colectados en estas áreas.

INTRODUCTION

This paper is the third in a series of descriptions of coral faunas from the Neogene of the Northern Dominican Republic, the first two being those of Foster (1986, 1987), and is one of many coral revisions anticipated from the large, multidisciplinary project of which they are part. This project surveys in depth the paleontology and stratigraphy of the Neogene of the Cibao Valley region of the Dominican Republic (Text-fig. 1). The specific history of Neogene coral research in the Dominican Republic has been reviewed by Foster (1986), and the background, lithology, age, and rationale of the entire project have been presented by Saunders, Jung, and Biju-Duval (1986). This information will not be repeated, except to note that there are few places in the Caribbean Neogene outside the Dominican Republic where the macrofauna is so diverse and well-preserved in continuous sequence as to allow a meaningful examination of total assemblages and their relation to paleoenvironment and time. It is hoped that our contribution will add to the growing knowledge about this region and eventually will contribute to a better understanding of the evolution, zoogeography, and paleoecology of this region.

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viding invaluable advice regarding the lithology of the area and the proper format for this paper.

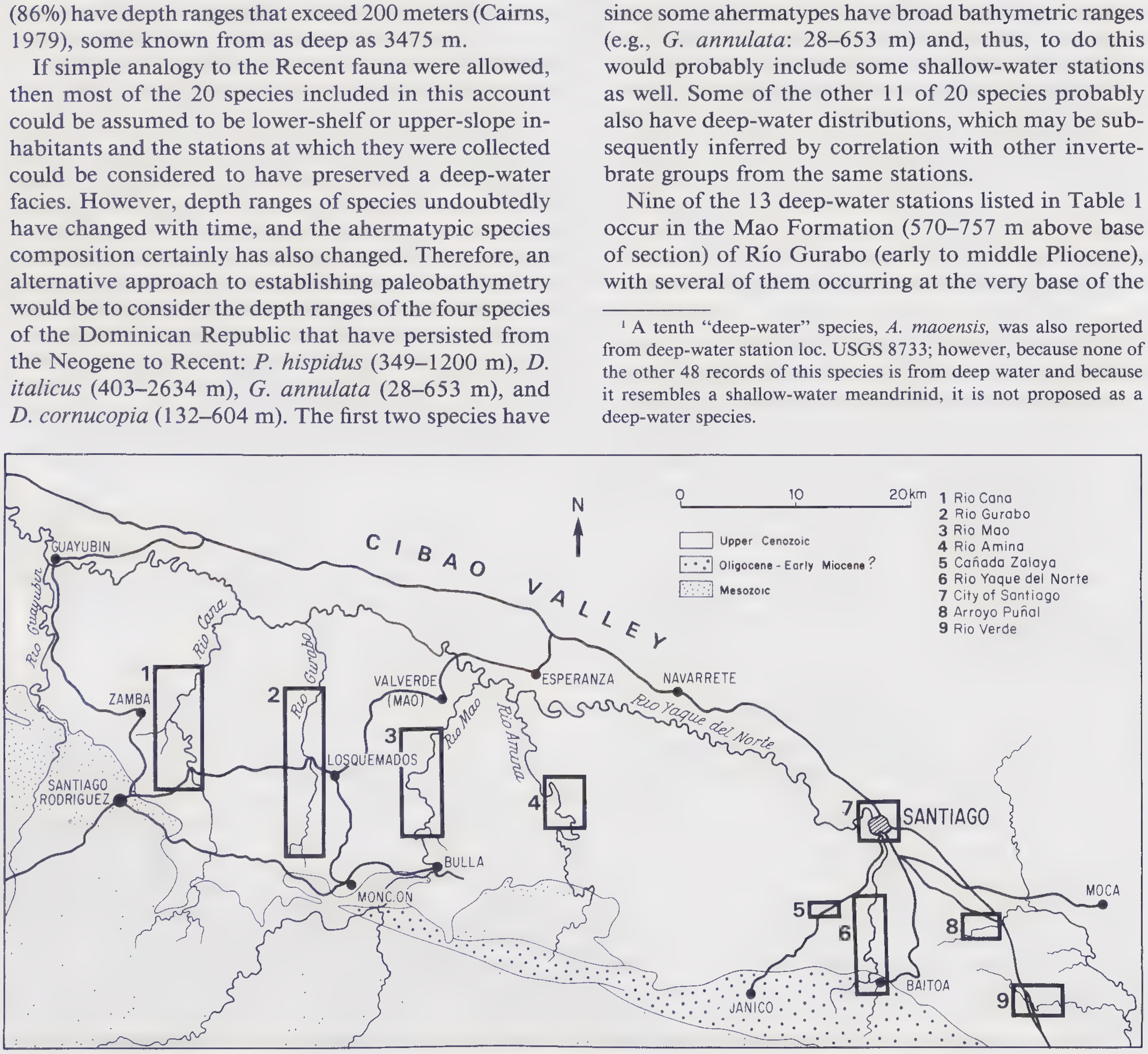
PALEOECOLOGY

The suborders Caryophylliina and Dendrophylliina contain primarily azooxanthellate ahermatypic species, which are generally associated with deep-water environments. For instance, of the 109 species of Recent western Atlantic Scleractinia in these two suborders (56% of the 194 species of Scleractinia known from the western Atlantic [Cairns, 1979]), only one is a hermatypic zooxanthellate [*Eusmilia fastigiata* (Pallas, 1766)], the remainder being ahermatypic azooxanthellates. Ninety-three of these remaining 108 species (86%) have depth ranges that exceed 200 meters (Cairns, 1979), some known from as deep as 3475 m.

If simple analogy to the Recent fauna were allowed, then most of the 20 species included in this account could be assumed to be lower-shelf or upper-slope inhabitants and the stations at which they were collected could be considered to have preserved a deep-water facies. However, depth ranges of species undoubtedly have changed with time, and the ahermatypic species composition certainly has also changed. Therefore, an alternative approach to establishing paleobathymetry would be to consider the depth ranges of the four species of the Dominican Republic that have persisted from the Neogene to Recent: *P. hispidus* (349–1200 m), *D. italicus* (403–2634 m), *G. annulata* (28–653 m), and *D. cornucopia* (132–604 m). The first two species have depth ranges that are exclusively deep-water (*i.e.,* exclusively deeper than 200 m), having been collected at 13 localities (Table 1). In addition to these two species, seven[1] other species were collected at these 13 stations (Table 2), the implication being that these latter species probably had bathymetric ranges that were at least as deep as the shallowest depth range of *P. hispidus* and *D. italicus* (*i.e.,* 350–400 m). Further support for this hypothesis includes a list of depth ranges of the Recent Caribbean counterparts to all nine species (Table 2), which, for the most part, have upper continental slope ranges. It was considered inadvisable to retroextrapolate by inferring that all stations at which these additional seven species occurred were also deep-water, since some ahermatypes have broad bathymetric ranges (e.g., *G. annulata*: 28–653 m) and, thus, to do this would probably include some shallow-water stations as well. Some of the other 11 of 20 species probably also have deep-water distributions, which may be subsequently inferred by correlation with other invertebrate groups from the same stations.

Nine of the 13 deep-water stations listed in Table 1 occur in the Mao Formation (570–757 m above base of section) of Río Gurabo (early to middle Pliocene), with several of them occurring at the very base of the

[1] A tenth "deep-water" species, *A. maoensis,* was also reported from deep-water station loc. USGS 8733; however, because none of the other 48 records of this species is from deep water and because it resembles a shallow-water meandrinid, it is not proposed as a deep-water species.



Text-figure 1.—Map indicating the location of river sections sampled. Specimens reported in this paper were collected in five sections: (1) Río Cana, (2) Río Gurabo, (3) Río Mao, (4) Río Amina, and (6) Río Yaque del Norte (map from Saunders, Jung, and Biju-Duval, 1986).

Table 1.—Localities at which *P. hispidus* and *D. italicus* were collected (therefore presumed to be deep-water environments [over 200 m]).

Locality	*Section*	*Formation*	*Level above Base of Section (meters)*	*Species Collected*
NMB 15823	Río Gurabo	Mao	672	*P. hispidus*
NMB 15828	Río Gurabo	Mao	713	*P. hispidus*
NMB 15829	Río Gurabo	Mao	757	*P. hispidus*
NMB 15995	Río Gurabo	Mao	570	*P. hispidus*
NMB 16016	Río Gurabo	Mao	580	*P. hispidus*
NMB 16023	Río Gurabo	Mao	640	*P. hispidus*
NMB 16036	Río Gurabo	Mao	660	*P. hispidus*
NMB 16038	Río Gurabo	Mao	660	*P. hispidus*
USGS 8735	Río Gurabo	Mao	660	*P. hispidus, D. cornucopia, T. duncani*
USGS 8702	Río Yaque del Norte	?Baitoa	?	*D. italicus, A. alatus*
USGS 8726	Río Yaque del Norte	?Baitoa	?	*P. hispidus, A. alatus*
USGS 8733	Río Mao	?Gurabo	?	*P. hispidus, D. cornucopia, Flabellum* sp., *A. profunda, A. exarata, A. maoensis*
TU 1227A	Arroyo Zalaya	?Gurabo	?	*P. hispidus, G.* sp. cf. *G. annulata, A. alatus*

Mao Formation. Two stations (loc. USGS 8702 and loc. USGS 8726) occur in the ?Baitoa Formation of Río Yaque del Norte, which is early to mid-Miocene; one station (loc. USGS 8733) occurs in the ?Gurabo Formation of Río Mao; and one station (loc. TU 1227A) occurs in the ?Gurabo Formation of Arroyo Zalaya.

Twelve of the 20 species reported in this paper are known only from the Dominican Republic but are not necessarily considered to be endemic to this island. Future collecting from the Caribbean Neogene will undoubtedly extend the distributions of many, if not all, of these species.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

The Dominican Republic Neogene Scleractinia examined in this study were obtained from four institutions, here listed in decreasing order of specimens available: NMB, NMNH, TU, and BM(NH). Most of the specimens from NMNH (collections of the U. S. Geological Survey) were previously reported by Vaughan (1919), Vaughan and Woodring (1921), and Vaughan and Hoffmeister (1925), whereas the BM(NH) specimens were reported by Duncan (1863, 1864, 1867, 1868), altogether resulting in records of 12 species in the suborders Caryophylliina and Dendrophylliina. Reports of specimens from NMB and TU have added eight new records of these taxa to the Dominican Republic Neogene (see *Checklist* herein), including four new species. Altogether, new specimens were available for 15 of the 20 taxa now known from this fauna. The five species of which additional specimens were not obtained [*P. henekeni* (Duncan, 1863), *D. italicus* (Michelotti, 1838), *D. dominicensis* (Vaughan, 1925), *A. compressa* Vaughan, 1925, and *A. duncani* Vaughan, 1925] are nonetheless included in this paper for completeness. Instead of giving a full description of these five species, we have provided diagnoses based on a reexamination of type-material and/or topotypic specimens, or, in one case, on specimens subsequently collected from an area other than the Dominican Republic.

Table 2.—Species believed to occur in deep water, and depth ranges of their Recent counterparts.

Dominican Republic Neogene Species	*Recent Caribbean Counterparts and Depth Ranges*
Antillocyathus alatus	none
Trochocyathus duncani	*T. rawsonii* (82–622 m)
Deltocyathus italicus	*D.* sp. cf. *D. italicus* (403–2634 m)
Asterosmilia exarata	*A. marchadi* (32–229 m)
Asterosmilia profunda	none
?*Flabellum* sp.	*F. atlanticum* (357–618 m)
Pourtalocyathus hispidus	*P. hispidus* (349–1200 m)
Guynia sp. cf. *G. annulata*	*G. annulata* (28–653 m)
Dendrophyllia cornucopia	*D. cornucopia* (132–604 m)

The higher-level classification used follows Wells (1956). Definitions of most terms can also be found there; however, several additional terms are defined here.

The ratio of the greater calicular diameter to the lesser calicular diameter, abbreviated *gcd:lcd,* is used in some species accounts. The *lateral thecal edges* are the two narrow thecal edges of an elliptical calice, *i.e.,* the part of the theca and calice intersected by the greater calicular axis. The *lateral thecal faces* are the two broad edges of an elliptical calice, *i.e.,* the parts of the theca and calice intersected by the lesser calicular diameter (Text-fig. 2). The two *principal costae* and *septa* are those aligned with the greater calicular axis along the lateral thecal edges. *Cycles of septa, costae, and pali* are indicated numerically following the capital letters **S**, **C**, and **P**, respectively. A species or specimen with five complete cycles of septa (96 septa), the first three cycles equal in exsertness and width and the remaining two cycles progressively smaller, is indicated by the formula: **S**1–3>**S**4>**S**5. **S**4+ indicates that in addi-

tion to a full fourth cycle of septa, some septa of the fifth cycle are present. When symmetry is not hexameral, as in *Antillocyathus* Wells, 1937, the septa are referred to as groups of equal-sized septa, termed *primary, secondary,* etc.

The synonymies are complete for all but five species, these five species having references to more complete synonymies. A question mark preceding a synonym entry indicates a doubtful identification not verified by examination of the specimen.

The convention *cf.* is used for two of the 20 species identified [i.e., *C. duodecimcostatus* (Goldfuss, 1826) and *G. annulata* Duncan, 1872] to imply that the Dominican Republic specimens are most similar, if not identical, to these species, but that not enough specimens are available to make a definitive statement.

The type-specimens of 16 of the 19 described species were examined. The types of *C. duodecimcostatus, D. italicus,* and *D. dominicensis* are lost; however, reference specimens of these three species were examined.

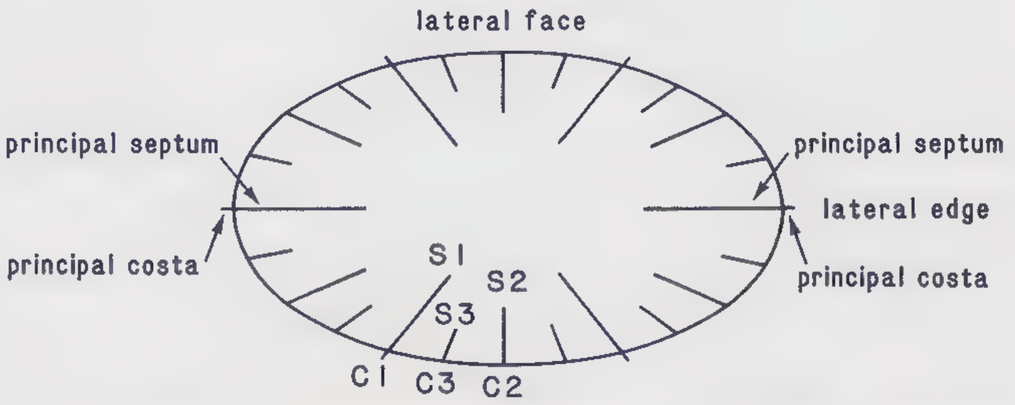
In the *Material* section, localities (locs.) NMB 15803–17273 are cited. Unless otherwise indicated, specimens may be assumed to be deposited at the collecting institution: four-digit catalog numbers prefaced with a D refer to the NMB collection. The number in parentheses in the *Material* sections indicates the number of specimens examined; if accompanied by a museum catalog number, this museum number refers to all specimens represented by the number in parentheses. Information on localities and ages of collection sites are found in Saunders, Jung, and Biju-Duval (1986) for NMB localities; Vaughan *et al.* (1921) for the USGS localities; and Vokes (1979) for TU localities.

In the *Comparison* sections of the species accounts, the Dominican Republic species are usually first compared to the Neogene congeners from the Dominican Republic and Caribbean; next, to other European congeners (as reviewed by Chevalier, 1961); and finally, to Caribbean Recent congeners (as reviewed by Cairns, 1979). In most cases these related species were examined and some are illustrated in the plates.

Philosophical Considerations

Interspecific skeletal variation has plagued coral systematists for over a century (Veron and Pichon, 1976). The high phenotypic plasticity of the coralla, easily modified by environmental conditions, caused such difficulty in determining species boundaries that Bernard (1903) departed from Linnaean binomial nomenclature for a noncommittal geographic numbering system. Although many nonskeletal characters of Scleractinia can be used for taxonomy at the species level (see review by Lang, 1984), the identification and classification of both Recent and fossil Scleractinia depend almost entirely on skeletal characters, much to the delight of the paleontologist, and in most cases the skeleton provides an adequate set of characters to differentiate species and to form a higher classification. The species concept used in this paper is that of the morphospecies, first formalized for Scleractinia by Vaughan (1907, p. 4) as: " . . . a group of individuals connected among themselves by intergrading characters and separated by distinct lacunae from all other individuals or groups of individuals." It is obviously advantageous to have as many specimens as possible of each species in order to elevate diagnoses and descriptions from the typological level to a biological or population level, including an analysis of variation. For some species, e.g., *Antillocyathus maoensis* (Vaughan, 1925), it was possible to study variation, but for others, e.g., *Asterosmilia duncani* Vaughan, 1925, and *A. compressa* Vaughan, 1925, the treatment was literally typological, since only the types of these species are known. Basically, our systematic philosophy was to: obtain as many specimens as possible (in this case, 1590) for a study of intraspecific variation; examine all extant types of species previously described from the Dominican Republic; study closely-related species in both the Neogene and Recent of the Caribbean and Mediterranean; and qualify our identifications if specimens were poorly preserved or few in number.

Some of the discriminating characters useful at the species level were: (1) shape and size of corallum and resultant shape of calice; (2) number of septa at a particular calicular diameter; (3) relative degree of exsertness of septal cycles; (4) costal development; and (5) pali and paliform lobe configuration. The character of columella shape, usually consistent at the generic level, was found to be variable within species of *Asterosmilia* Duncan, 1867. Thin-sections of coralla and scanning electron microscopy of septal faces were prepared for some species when adequate numbers of specimens were available, but little of systematic value was obtained from these approaches.



Text-figure 2.—Diagram of cross-section of a calice illustrating some of the morphological terms used in the text. **S** = septa, **C** = costae, numbers indicate respective septal or costal cycle.

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

BM(NH): British Museum (Natural History), London, England, U.K.
Gabb: Gabb Collection, deposited at the Museum of Comparative Zoology, Harvard College, Cambridge, MA, U.S.A.
MCZ: Museum of Comparative Zoology, Harvard College, Cambridge, MA, U.S.A.
MNHNP: Muséum national d'Histoire naturelle, Paris, France
NMB: Naturhistorisches Museum, Basel, Switzerland
NMNH: United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
TU: Tulane University, New Orleans, LA, U.S.A.
USGS: United States Geological Survey (specimens deposited at the NMNH)
USNM: United States National Museum of Natural History (specimens deposited at the NMNH)

CHECKLIST OF NEOGENE CARYOPHYLLIINA AND DENDROPHYLLIINA FROM THE DOMINICAN REPUBLIC

Suborder Caryophylliina Vaughan and Wells, 1943
Superfamily Caryophylliicae Dana, 1846
Family Caryophylliidae Dana, 1846
Subfamily Caryophylliinae Dana, 1846
Antillocyathus maoensis (Vaughan *in* Vaughan and Hoffmeister, 1925)
**Antillocyathus alatus,* n. sp.
Antillocyathus cristatus (Vaughan *in* Vaughan and Hoffmeister, 1925)
**Trochocyathus* (*Paratrochocyathus*) *chevalieri,* n. sp.
**Trochocyathus* (*Paratrochocyathus*) *duncani,* n. sp.
Ceratotrochus (*Edwardsotrochus*) sp. cf. *C. duodecimcostatus* (Goldfuss, 1826)
Paracyathus henekeni (Duncan, 1863)
**Paracyathus sinuosus,* n. sp.
Deltocyathus italicus (Michelotti, 1838)
Subfamily Turbinoliinae Milne-Edwards and Haime, 1848b
**Sphenotrochus* (*Eusthenotrochus*) *senni* Wells, 1945
Dominicotrochus dominicensis (Vaughan *in* Vaughan and Hoffmeister, 1925)
Subfamily Parasmiliinae Vaughan and Wells, 1943
Asterosmilia abnormalis (Duncan, 1864)
Asterosmilia exarata Duncan, 1867
Asterosmilia profunda (Duncan, 1864)
Asterosmilia duncani Vaughan *in* Vaughan and Hoffmeister, 1925
Asterosmilia compressa Vaughan *in* Vaughan and Hoffmeister, 1925
Superfamily Flabellicae Bourne, 1905
Family Flabellidae Bourne, 1905
?*Flabellum* sp.
Family Guyniidae Hickson, 1910
**Pourtalocyathus hispidus* (Pourtalès, 1878)
**Guynia* sp. cf. *G. annulata* Duncan, 1872
Suborder Dendrophylliina Vaughan and Wells, 1943
Family Dendrophylliidae Gray, 1847
**Dendrophyllia cornucopia* Pourtalès, 1871

Suborder **CARYOPHYLLIINA** Vaughan and Wells, 1943

Superfamily **CARYOPHYLLIICAE** Dana, 1846

Family **CARYOPHYLLIIDAE** Dana, 1846

Subfamily **CARYOPHYLLIINAE** Dana, 1846

Genus **ANTILLOCYATHUS** Wells, 1937

Diagnosis.—Solitary; corallum strongly compressed, almost flabellate. Septotheca strongly costate. Pali before S3 in one crown (or before penultimate cycle of septa when more than four septal cycles or when hexameral symmetry obscured). Columella elongate, sublamellar. Dissepiments absent or rare.

Type-species.—*Placocyathus maoensis* Vaughan *in* Vaughan and Hoffmeister, 1925, by original designation.

Discussion.—Other species placed in *Placocyathus* Milne-Edwards and Haime, 1848b, by Duncan and Vaughan, other than the monocentric *P. maoensis* Vaughan *in* Vaughan and Hoffmeister, 1925, and *P. cristatus* Vaughan *in* Vaughan and Hoffmeister, 1925 (referred to as *Antillocyathus* in this paper), include *P. barretti* Duncan, 1863; *P. variabilis* Duncan, 1864; *P. alveolus* Duncan, 1863; and *P. costatus* Duncan, 1864. All of these forms in their early stages resemble *Antillocyathus* Wells, 1937, in shape but with increase in size become compressed, elongate, continuous or sinuous polycentric calicular series. They have dissepiments and paliform lobes, rather than true pali of *Antillocyathus,* before the second and third rank septa, and notably, continuous principal costae ("costae of symmetry"), the persistent primary directive costae. These are the characters of *Meandrina* Lamarck, 1801 which, however, lacks the continuous principal costae and has lateral calicular lobes. The general morphology of these polycentric species of *Placocyathus* is strikingly similar to that of species of the short-lived late Cretaceous genus *Phyllosmilia* Fromentel, 1862, ex-

* New record for the Dominican Republic.

cept for the presence of paliform lobes. *Placocyathus barretti, P. variabilis, P. costatus,* and *P. alveolus* thus appear to represent a distinct generic group meriting further study.

Distribution.—Miocene, West Indies.

Antillocyathus maoensis (Vaughan, 1925)
Plate 8, figures 1–7, 13

Placocyathus maoensis Vaughan *in* Vaughan and Hoffmeister, 1925, pp. 317–318, pl. 1, figs. 3–10; Felix, 1927, p. 444.
Antillocyathus maoensis (Vaughan). Wells, 1937, p. 11; Weisbord, 1973, p. 62; ?Ricart y Menéndez, 1983, part (figs. 1, 13–15).
Not *Antillocyathus maoensis* (Vaughan). Frost and Langenheim, 1974, pp. 300–301; Ricart y Menéndez, 1982a, pp. 129–130, figs. 1–4.
?*Antillocyathus maoensis* (Vaughan). Ricart y Menéndez, 1982b, pp. 133–135, figs. 1–9.

Description.—Corallum straight and flabellate, narrowing to a short, slender pedicel about 1.2 mm in diameter, which is invariably detached from substrate. From side view, corallum shaped as an isosceles triangle, with the variable angle, the pedicel, ranging from 60° to 80°. Largest specimen examined (USNM 64271 from loc. USGS 8545) 23 × 9 mm in calicular diameter and 25 mm in height; however, most specimens 13–18 mm in **gcd**. Calice elongate with parallel to slightly concave lateral faces. Ratio of **gcd:lcd** ranges from 1.75 to 2.50; this ratio increasing with increase of the **gcd**, implying a greater flattening of the calice with growth. The two lateral edge costae, those associated with the narrow thecal edges, often ridged and crested for basal 4–10 mm. Otherwise, costae usually low, rounded, and granulated, about 0.30 mm wide and separated by shallow grooves. Occasionally **C**1 are slightly ridged. Shallow transverse grooves about 1.75 mm wide periodically encircle theca (Pl. 8, fig. 1).

Septa not arranged hexamerally; instead, 19–24 large primary septa, an equal number of secondary septa, twice this number of tertiary septa, and often several pairs of quaternary septa fill the calice. Based on 24 well-preserved coralla, the most common number of primary septa is 20 (found in 16 of the coralla), followed by 21 primary septa in four coralla, 23 in two, 19 in one, and 24 in one. Number of septa per corallum ranges from 78 to 104, the one with 104 septa having 24 primary septa and four pairs of quaternary septa. Most common numbers of septa per corallum were 84 and 82, reflecting a corallum with 20 primary septa, a full complement of secondary and tertiary septa, and two (or one pair of) quaternary septa, respectively. When present, quaternary septa occur in pairs and usually in half-systems directly adjacent to the two principal septa. Primary septa highly exsert, about 0.55 mm wide, with straight vertical inner edges, which fuse to columella lower in fossa. Secondary septa about half as large and much less exsert, about 0.25 mm wide. Tertiary septa smaller but as exsert as secondary septa, about 0.10 mm thick. Quaternary septa rudimentary. Inner edges of all septa simple, not bifurcate. Septal faces covered with sharp granules up to 0.13 mm in height, arranged both in rows parallel to the inner septal edge and in lines perpendicular to septal edge (following the trabeculae), the latter arrangement more apparent on distal septal edge, the former more common on septal face.

Fossa elongate and relatively shallow. Lower corallum filled with stereome; no endotheca. A distinct crown of rounded pali present, one before each secondary septum and a smaller one before each tertiary septum that is flanked by quaternary septa. Occasionally a small paliform lobe occurs before primary septa. Pali 0.75–1.40 mm wide, separated from secondary septa by a deep notch. Inner edges of pali vertical and straight. Columella elongate (up to 7 mm long and 0.6 mm wide), solid, and lamellar. Sides of columella covered with horizontal carinae of variable length. No "inner septa" (*sensu* Ricart y Menéndez, 1982a).

Diagnostic characters.—Hexameral symmetry usually not apparent (often 20 primary septa); high **gcd:lcd** (1.75–2.50); lateral corallum faces slightly concave.

Type-material.—The holotype, collected at loc. USGS 7785, is deposited at the NMNH (USNM 353644). It is 14.4 × 7.8 mm in calicular diameter, 15.8 mm in height, and has 78 septa (including 19 primary septa and one pair of quaternary septa). Three paratypes are deposited at the MCZ: one, unnumbered, appears in Vaughan (1925) as pl. 1, figs. 5–6; a second, MCZ 9267, is Vaughan's pl. 1, figs. 7–8; and a third, MCZ 9269, is Vaughan's pl. 1, figs.. 9–10. Two additional specimens labelled in Vaughan's handwriting as paratypes are deposited at the NMNH (USNM 68303 from loc. USGS 7776; and USNM 68304 from loc. USGS 7777) but because these were not cited by Vaughan (*in* Vaughan and Hoffmeister, 1925) as types, they are not considered as such.

Type-locality.—Loc. USGS 7785: Río Mao, Bluff 1 of Maury (?Cercado Formation), Dominican Republic, late Miocene.

Material.—Unnumbered NMB specimens from locs. NMB 15804 (2); 15805 (1); 15806 (26); 15807 (165); 15809 (13); 15810 (11); 15814 (4); 15836 (26); 15843 (1); 15855 (2); 15860 (3); 15863 (50); 15864 (80); 15865 (18); 15867 (2); 15869 (3); 15871 (1); 15883 (1); 15899 (1); 15964 (1); 16809 (4); 16810 (31); 16910 (12); USNM 64512 (25) from loc. NMB 15807; USNM 68303 (1) from loc. USGS 7776; USNM 68303 (2) from loc. USGS 7777; USNM 353644 (holotype) from loc. USGS 7785; USNM 64482 (11) from loc. USGS 8516; USNM 63072 (116) from loc. USGS 8519; USNM 64267 (1) from loc. USGS 8520; USNM 68424 (34) from loc. USGS 8521; USNM 64479 (7) from loc.

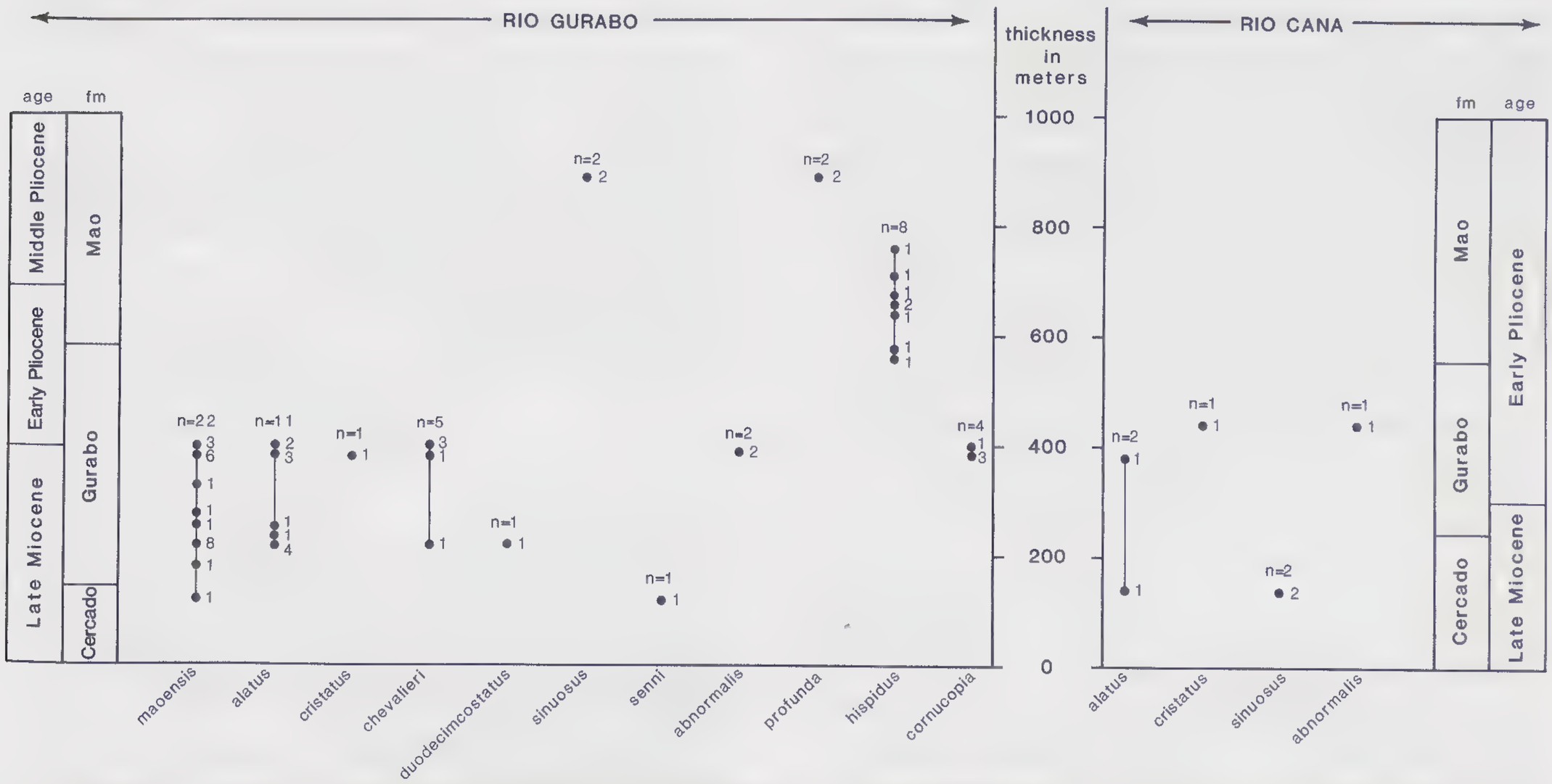
USGS 8522; USNM 64269 (3) from loc. USGS 8528; USNM 64481 (1) from loc. USGS 8537; USNM 64483 (3) from loc. USGS 8538; USNM 64271 (67) from loc. USGS 8545; USNM 64265 (8) from loc. USGS 8546; USNM 64270 (1) from loc. USGS 8547; USNM 64272 (2) from loc. USGS 8549; USNM 64268 (1) from loc. USGS 8727; USNM 64264 (1) from loc. USGS 8733; USNM 64266 (1) from loc. USGS 8734; unnumbered TU specimens from loc. TU 1210 (40); loc. TU 1211 (11); loc. TU 1213 (1); loc. TU 1225 (1); loc. TU 1231 (33); loc. TU 1277 (9); loc. TU 1278 (12); loc. TU 1359 (5); loc. TU 1451 (1); MCZ 9267, 9269 (paratypes).

Remarks.—Frost and Langenheim (1974) reported a single, poorly-preserved specimen of *A. maoensis* from the lower Miocene of Mexico; however, several elements of their description do not represent this species. First, their specimen had 79 septa arranged hexamerally. At the specimen size they reported, 79 septa would not be unusual, but hexameral symmetry and the relative sizes of the septa they reported (S1>S2>S3) are inconsistent with Dominican Republic specimens. Also, they reported paliform lobes before the first two cycles of septa but did not mention pali before the S3; this is quite different from typical specimens of *A. maoensis*. We seriously doubt the Mexican specimens are conspecific with *A. maoensis*.

Ricart y Menéndez wrote three papers on *Antillocyathus maoensis* from the Dominican Republic. His third and most detailed paper (Ricart y Menéndez, 1983) described and illustrated an unnamed species closely related to but different from *A. maoensis*. His first paper on inner septa of *A. maoensis* (Ricart y Menéndez, 1982a) also appears to describe this unnamed species. The second paper (Ricart y Menéndez, 1982b) is problematic from the point of view of synonymy because only columellar structures are illustrated; however, his figure 1 is consistent with the known columellar structure of *A. maoensis*.

Comparisons.—*Antillocyathus maoensis* is similar to *A. alatus*, n. sp. as discussed in the account of the latter species. There are no known Recent species of *Antillocyathus* nor is any species of this genus known from the European Miocene.

Occurrence.—Río Gurabo (Cercado and Gurabo formations) late Miocene to earliest Pliocene (Text-fig. 3): locs. NMB 15804, 15805, 15806, 15807, 15809, 15810, 15814, 15836, 15843, 15855, 15860, 15863, 15864, 15865, 15867, 15869, 15871, 15883, 15899, 15964, 16809, 16810, loc. USGS 7776, loc. USGS 7777, loc. USGS 8537, loc. USGS 8538, loc. USGS 8545, loc. USGS 8546, loc. USGS 8547, loc. USGS 8549, loc. USGS 8727, loc. TU 1210, loc. TU 1211, loc. TU 1213, loc. TU 1277, loc. TU 1278, loc. TU 1359. Río Mao (?Cercado Formation) late Miocene: loc. NMB 16910, loc. USGS 8519, loc. USGS 8520, loc. USGS 8521, loc. USGS 8522, loc. USGS 8528, loc. USGS 8733, loc. USGS 8734, loc. TU 1225. Río Amina: loc. USGS 8516. Arroyo Babosico (?Gurabo Formation): loc. TU 1451.



Text-figure 3.—Diagram showing the NMB records of species within the two stratigraphically well-documented river sections: Río Gurabo and Río Cana. "n" = total number of localities containing each species. Numbers to the right of points along each vertical line indicate the number of localities represented by each point.

Distribution.—Known only from the late Miocene to early Pliocene of the Dominican Republic from Río Gurabo, Río Mao, Río Amina, and Arroyo Babosico.

Antillocyathus alatus, new species
Plate 8, figures 8–12

Etymology.—The specific name *alatus* (Latin for "winged") refers to the alate principal costae of this species.

Description.—Corallum straight, trochoid to ceratoid, the lateral thecal edges becoming almost parallel in larger specimens (Pl. 8, fig. 10). Pedicel diameter about 1.2 mm, always detached from substrate. Largest specimen examined (NMB D 5879 from loc. NMB 16857; Pl. 8, fig. 10) 13.6 × 9.3 mm in calicular diameter and 17.9 mm in height, but most specimens 9.5–10.5 mm in **gcd** and 10–14 mm in height. Calice elliptical with straight to slightly convex lateral faces. Ratio of **gcd:lcd** ranges from 1.30 to 1.75. Two principal costae commonly ridged (alate) in lower half of corallum and may project as relatively large lateral crests. Other costae low, rounded, and granulated as in *A. maoensis*.

Septa not consistently hexamerally arranged. Below **gcd** of 10.5 mm there are usually 12 primary and secondary septa, 24 tertiary septa, and a variable number of quaternary septa (usually four pairs), often making a total of 56 septa. However, at a **gcd** between 11 and 13 mm there are usually 14 primary septa; at a **gcd** of over 13 mm, 16. Based on 19 well-preserved coralla, number of septa ranges from 52 to 72 (mode = 56). Primary septa moderately exsert, about 0.50 mm wide, with straight vertical inner edges. Secondary septa smaller, about three-fourths as exsert as primary septa, and about 0.25 mm wide. Tertiary septa smaller and less exsert than secondary septa. Quaternary septa, when present, most often occur in half-systems directly adjacent to principal septa. Inner edges of septa simple; not bifurcate. Septal granulation as in *A. maoensis*.

Fossa elongate and relatively shallow; no endotheca. Pali on inner edges of all secondary septa and those tertiary septa flanked by quaternary septa. Pali 0.6–1.4 mm wide, separated from septa by a deep notch. Columella elongate and lamellar, with a straight, sharp upper edge. Sides of columella covered with short horizontal carinae. No inner septa.

Diagnostic characters.—Rarely more than 16 moderately exsert septa and therefore less than 64 total septa per corallum; low **gcd:lcd** (1.30–1.75); upper thecal edges almost parallel.

Type-material.—Holotype: NMB D 5878, from loc. NMB 15871 (11.2 × 7.7 mm in calicular diameter, 13.1 mm in height, 66 septa with 14 primary septa). Paratypes: unnumbered NMB specimens from locs. NMB 15810 (3); 15812 (1); 15814 (4); 15860 (3); 15863 (3); 15871 (37); 15962 (4); 15964 (4); 16808 (5); 16809 (3); 16857 (4); 16862 (1); USNM 65481 (1) from loc. USGS 7776; USNM 63064 (2) from loc. USGS 8544; USNM 74683 (2) from loc. USGS 8549; USNM 63063 (7) from loc. USGS 8702; USNM 63061 (1) from loc. USGS 8726; USNM 63062 (1) from loc. USGS 8734.

Type-locality.—Loc. NMB 15871: Río Gurabo (Gurabo Formation: 220 m), lower Miocene.

Non-type material.—Unnumbered TU specimens from loc. TU 1227A (5); loc. TU 1277 (1).

Comparisons.—*Antillocyathus alatus,* n. sp. is very similar to *A. maoensis* (Vaughan, 1925) and might possibly be considered as a younger stage of the latter species; however, there are several consistent and non-overlapping differences that we feel justify a species distinction. First, *A. alatus* has a smaller and slightly differently-shaped corallum. Its lateral edges do not diverge with the regularity of *A. maoensis* and, in fact, are parallel in large specimens. Second, the corallum and calice of *A. alatus* is fuller than that of *A. maoensis,* exemplified by a lower **gcd:lcd** ratio and a fuller, more elliptical calicular outline. Third, *A. alatus* has fewer primary and total septa. And finally, there is a difference in the degree of septal exsertness between the two species, characterized by the highly-exsert primary septa of *A. maoensis* that extend far beyond the equally exsert secondary and tertiary septa *vs.* the moderately-exsert primary septa of *A. alatus* and the progressive decrease in exsertness of its higher-cycle septa.

Occurrence.—Río Gurabo (Gurabo Formation) late Miocene to earliest Pliocene (Text-fig. 3): locs. NMB 15871, 15810, 15812, 15814, 15860, 15863, 15871, 15962, 15964, 16808, 16809, loc. USGS 7776, loc. USGS 8544, loc. USGS 8549, loc. TU 1277. Río Cana (Gurabo Formation) late Miocene to early Pliocene (Text-fig. 3): locs. NMB 16857, 16862. Río Mao (?Cercado Formation) late Miocene: loc. USGS 8734. Río Yaque del Norte (?Gurabo Formation) late Miocene: loc. USGS 8702, loc. USGS 8726. Arroyo Zalaya (?Gurabo Formation): loc. TU 1227A.

Distribution.—Known only from the late Miocene to early Pliocene of the Dominican Republic from Río Gurabo, Río Cana, Río Mao, Río Yaque del Norte, and Arroyo Zalaya.

Antillocyathus cristatus (Vaughan, 1925)
Plate 8, figures 14–16

Placocyathus cristatus Vaughan *in* Vaughan and Hoffmeister, 1925, pp. 319–320, pl. 1, figs. 11–14; Felix, 1927, p. 443.
Antillocyathus cristatus (Vaughan). Wells, 1937, p. 12.

Description.—Corallum flabellate and slightly curved in plane of greater calicular axis, the calice oriented about 40° from original pedicel growth axis. Largest

specimen (NMB D 5882 from loc. NMB 15809) 43.5 mm in height; holotype (USNM 353643 from loc. USGS 7785) 22.7 × 13.4 mm in calicular diameter and 22.2 mm in height. Calice elliptical, with **gcd:lcd** ratios ranging from 1.61 to 1.69. On lower half of corallum, two ridged principal costae, some projecting as much as 2 mm; the principal costa of convex thecal edge usually more prominent. Otherwise, costae are of equal width and are low to slightly ridged. Shallow transverse grooves up to 2.0 mm wide periodically encircle theca.

In the only specimen preserved well enough to examine the septal number and structure (the holotype), there are 106 septa arranged in five cycles with five pairs of **S**6. **S**1–3 of equal size, having straight vertical thickened inner edges and exsert upper edges. **S**4–6 progressively smaller in size and exsertness.

Fossa elongate and relatively deep. No endothecal dissepiments. Narrow pali occur before septa of fourth (penultimate) cycle; however, the poor preservation of all specimens does not allow more detailed observations. Columella elongate, spongy, or lamellar; that of holotype 10.5 mm long and 1.2 mm wide.

Diagnostic characters.—Corallum slightly curved in plane of greater calicular axis; pairs of **S**6 present.

Type-material.—USNM 353643 (holotype) from loc. USGS 7785. Measurements of holotype are given in the description.

Type-locality.—Loc. USGS 7785: Río Mao, Bluff 1 of Maury (?Cercado Formation) Dominican Republic, late Miocene.

Material.—USNM 353645 (holotype) from loc. USGS 7785; unnumbered NMB specimens from locs. NMB 15809 (1); 16868 (1); MCZ 9269 [Gabb Collection] (1) (see Vaughan and Hoffmeister, 1925, pl. 1, figs. 12–13); unnumbered TU specimens from loc. TU 1205 (1); loc. TU 1278 (1); loc. TU 1436 (6).

Remarks.—Vaughan's original description is quite complete; however, we disagree with him on two minor details. The five pairs of **S**6 are not restricted to the lateral edge half-systems but also occur in half-systems along the lateral faces. Also, the **S**3 are approximately the same size as the **S**1+2.

Comparisons.—*Antillocyathus cristatus* is easily distinguished from *A. maoensis* (Vaughan, 1925) and *A. alatus,* n. sp. by its larger size, greater number of septa, and its curved corallum. It is similar in growth form and costal ornamentation to *Asterosmilia abnormalis* Duncan, 1864, but can be distinguished by its lack of dissepiments, more robust corallum, and larger **gcd: lcd** ratio.

Occurrence.—Río Gurabo (Gurabo Formation) late Miocene (Text-fig. 3): loc. NMB 15809, loc. TU 1278. Río Cana (Gurabo Formation) early Pliocene (Text-fig. 3): loc. NMB 16868. Río Mao (?Cercado Formation) late Miocene: loc. USGS 7785. Río Yaque del Norte at Santiago de los Caballeros (?Gurabo Formation): loc. TU 1205.

Distribution.—Known only from the late Miocene to early Pliocene of the Dominican Republic from Río Gurabo, Río Cana, Río Mao, and Río Yaque del Norte.

Genus **TROCHOCYATHUS**
Milne-Edwards and Haime, 1848b

Diagnosis.—Solitary; corallum bowl-shaped, ceratoid, or turbinate; free or attached. Septotheca costate. Discrete pali arranged in two crowns before all but last cycle of septa. Columella fascicular, spongy, or crispate. No endotheca.

Subgenus **PARATROCHOCYATHUS** Alloiteau, 1958

Diagnosis.—*Trochocyathus* in which the columella is an elliptical field of papillae, not lamellar or aligned papillae.

Type-species.—*Paratrochocyathus collingnoni* Alloiteau, 1958, by original designation.

Distribution.—Miocene of Italy, Madagascar, and West Indies; Recent of West Indies.

Trochocyathus (Paratrochocyathus) chevalieri, new species
Plate 8, figures 19–21

?*Trochocyathus cornucopia* (Michelotti). Duncan, 1863, pp. 428, 450; Duncan, 1868, pp. 22, 27.

Etymology.—This species is named in honor of Jean-Pierre Chevalier (1926–1981).

Description.—Corallum ceratoid, straight to slightly curved, narrowing to a slender pedicel about 1.4 mm in diameter. Holotype (NMB D 5884 from loc. NMB 15836) 10.3 × 8.4 mm in calicular diameter (**gcd:lcd** = 1.22) and 13.5 mm in height; largest specimen (unnumbered specimen from loc. TU 1205) 21.2 mm in height. Corallum white to light reddish-brown; the colored corallum most common on broken surfaces of well-preserved specimens. Costae about 0.6 mm wide and equal in width; costae low and granular.

Septa hexamerally arranged in four cycles. **S**1+2 equal in size and exsertness, the higher cycle septa progressively smaller. **S**4 usually fuse to adjacent **S**3 below palar level through several digitiform processes. **S**1+2 extend only about halfway to columella, the other half occupied by their pali.

Fossa shallow, containing a well-developed columella and two crowns of prominent pali. Pali occur before first three cycles of septa, the **P**1–2 usually half as large as the **P**3 (0.75 mm *vs.* 1.5 mm wide, respectively). Inner edges of all pali terminate at same distance into the calice, directly adjacent to columella.

Columella papillose; composed of an elliptical field of 15–30 slender, granular, irregularly-shaped rods arranged in a compact mass.

Diagnostic characters.—Columella robust; **P**3 large.

Type-material.—Holotype: NMB D 5884 from loc. NMB 15836. Paratypes: unnumbered NMB specimens from locs. NMB 15836 (4); 15804 (8); 15809 (19); 15813 (1); NMB D 5883 (1) from loc. NMB 15816; USNM 74682 (5) from loc. NMB 15809.

Type-locality.—Loc. NMB 5836: Río Gurabo (Gurabo Formation: 380 m above base of section), late Miocene.

Non-type material.—Unnumbered TU specimens from loc. TU 1205 (16); loc. TU 1210 (1); loc. TU 1211 (8); loc. TU 1213 (1); loc. TU 1278 (1); loc. TU 1359 (47).

Remarks.—Duncan (1863, 1868) listed the European Miocene species *Trochocyathus cornucopia* (Michelotti, 1838) from the Dominican Republic, but did not describe or illustrate the specimen. Such a specimen could not be found at the British Museum. *Trochocyathus* (*Paratrochocyathus*) *chevalieri* is similar in size and shape to *T. cornucopia* and therefore might have been the species Duncan listed; however, true *T. cornucopia,* now placed in the subgenus *Caryophyllia* (*Ceratocyathus*) Seguenza, 1864, has pentameral symmetry and pali only before the **S**3.

Comparisons.—*Trochocyathus chevalieri* belongs to the subgenus *Paratrochocyathus* Alloiteau, 1958; Chevalier (1961) listed eight species in this subgenus (known primarily from the Miocene of Italy and Madagascar) and implied that many more species from the Tertiary and Recent may also belong to this subgenus. Of the eight listed by Chevalier, *T. chevalieri* is most similar to *T.* (*P.*) *acutus* Chevalier, 1961, but can be distinguished by its much more robust columella and large **P**3.

Three Recent species of *T.* (*Paratrochocyathus*) occur in the Caribbean: *T.* (*P.*) *rawsonii* Pourtalès, 1874; *T.* (*P.*) *fossulus* Cairns, 1979; and *T.* (*P.*) *fasciatus* Cairns, 1979. They are easily distinguished from *T.* (*P.*) *chevalieri* by their growth form: *T.* (*P.*) *rawsonii* is bowl-shaped to turbinate, whereas the other two species are ceratoid but firmly attached to the substrate. They are all relatively deep-water species, known from 82 to 622 m (Cairns, 1979).

Occurrence.—Río Gurabo (Gurabo Formation) late Miocene to earliest Pliocene (Text-fig. 3): locs. NMB 15804, 15809, 15813, 15816, 15836, loc. TU 1210, loc. TU 1211, loc. TU 1213, loc. TU 1278. Río Gurabo (?Cercado Formation) late Miocene: loc. TU 1359. Río Yaque del Norte at Santiago de los Caballeros (?Gurabo Formation): loc. TU 1205.

Distribution.—Known only from the late Miocene to early Pliocene of the Dominican Republic from Río Gurabo and Río Yaque del Norte.

Trochocyathus (Paratrochocyathus) duncani, new species

Plate 8, figures 22, 23

Etymology.—This species is named in honor of Peter Martin Duncan (1824–1891).

Description.—Corallum ceratoid to trochoid and straight. Pedicel of single attached corallum (USNM 63042 from loc. USGS 8735) 4.5 mm in diameter and straight; pedicels of other five unattached coralla (USNM 74684 [holotype] and USNM 74685 [four paratypes] from loc. TU 1208) 2.0–2.5 mm in diameter and curved. Holotype (largest specimen) 18.2 mm in calicular diameter and 29.1 mm in height. Calice round. Costae equal in width (about 0.8–0.9 mm across) and convex to ridged, separated by deep intercostal grooves. Costae granular.

Septa hexamerally arranged in four complete cycles with some pairs of **S**5. Of the four well-preserved coralla, septal number varied from 48 to 54. **S**1>**S**2>**S**3>**S**4. Inner edges of **S**1–3 moderately sinuous. Degree of septal exsertness unknown.

Fossa shallow. **P**1 small, about 1.0 mm wide, extending to columella. **P**2 about 1.5 mm wide, projecting higher in fossa, and also extending to columella. Pairs of **P**3 flank each **P**2, the **P**3 about same size and height as **P**2 but recessed from columella. Columella composed of a field of six to 10 granulated pillars terminating below level of **P**1.

Diagnostic characters.—Ceratoid to trochoid corallum; 48–54 septa; **P**1<**P**2=**P**3.

Type-material.—Holotype: USNM 74684 from loc. TU 1208. Paratypes: USNM 74685 (4) from loc. TU 1208; USNM 63042 (1) from loc. USGS 8735.

Type-locality.—Loc. TU 1208: Mao Adentro Limestone, roadcut, both sides of highway from Mao to Los Quemados, at ridge 4 km east of Los Quemados.

Comparisons.—*Trochocyathus* (*Paratrochocyathus*) *duncani,* n. sp. is easily distinguished from *T.* (*P.*) *chevalieri,* n. sp. by its larger size, round calice, and different palar configuration. In the European Tertiary it is most similar to *T. imparipartitus* (Milne-Edwards and Haime, 1848b) from the upper Miocene of Italy (see Chevalier, 1961, p. 313), but can be distinguished by its round calice and lesser number of septa at a corresponding size. Within the Caribbean, *T.* (*P.*) *duncani* is very similar to *T.* (*P.*) *rawsonii* Pourtalès, 1874, particularly regarding calice shape and septal, palar, and columellar shapes and configuration. The only differences separating these two species are the lack of epitheca on *T.* (*P.*) *duncani* and its more slender, often ceratoid corallum.

Occurrence.—Río Gurabo (Mao Formation) early Pliocene: loc. USGS 8735. Mao Adentro Limestone: loc. TU 1208.

Distribution.—Known only from the early Pliocene "Mao Adentro Limestone" of the Dominican Republic, from Río Gurabo.

Genus **CERATOTROCHUS** Milne-Edwards and Haime, 1848b

Diagnosis.—Solitary; corallum trochoid; fixed or free. Septotheca costate. Paliform lobes before **S1+2**. Columella fascicular. No endotheca.

Subgenus **EDWARDSOTROCHUS** Chevalier, 1961

Diagnosis.—*Ceratotrochus* in which the columella is composed of numerous flattened horizontal paliform lobes, not vertical fascicles as in the nominal subgenus.

Type-species.—*Turbinolia duodecimcostata* Goldfuss, 1826, by original designation.

Distribution.—Miocene and Pliocene of Europe and west Africa, ?Azores; Miocene of West Indies.

Ceratotrochus (Edwardsotrochus) species cf. **C. (E.) duodecimcostatus** (Goldfuss, 1826)
Plate 9, figures 1, 2

Turbinolia duodecimcostata Goldfuss, 1826, p. 52, pl. 15, fig. 6.
Ceratotrochus duodecimcostatus (Goldfuss). Duncan, 1864, p. 22; Duncan, 1868, pp. 23, 27; Felix, 1927, pp. 395–396; Felix, 1929, p. 568.
Ceratotrochus duodecim-costatus (Goldfuss). Vaughan, 1919, p. 213.
Ceratotrochus (*Edwardsotrochus*) *duodecimcostatus* (Goldfuss). Chevalier, 1961, pp. 359–360, text-figs. 125–128 (synonymy).

Description of Dominican Republic specimens.—Corallum ceratoid to trochoid, straight to very slightly curved in plane of **gcd**. Largest specimen [BM(NH) 28819] 40 mm in height. Ratio of **gcd:lcd** = 1.38–1.50. Pedicel diameter about 1.8 mm. **C**1–2 very prominent for length of theca, projecting up to 1.5 mm as thin ridges about 0.6 mm wide. **C**3–5 low ridges or flat.

Septa hexamerally arranged in five incomplete cycles. The only specimen for which septal number could be determined (Pl. 9, fig. 2, NMB D 5886 from loc. NMB 15836) has 84 septa, lacking both pairs of **S**5 in two half-systems and lacking one pair of **S**5 in two other half-systems. The poor preservation of the specimens did not allow observation of the septal sizes, fossa, pali, and columellar structures.

Diagnostic characters.—**C**1–2 thin exsert ridges; corallum slightly curved; fifth septal cycle usually incomplete.

Type-material and type-locality.—The holotype, from the Pliocene of Plaisance, Italy, is lost (Chevalier, 1961).

Material.—Four unnumbered specimens from loc. NMB 15836; BM(NH) 28819 (1), Duncan's (1864) specimen from Angostina, Dominican Republic; unnumbered TU specimens from loc. TU 1225 (2); loc. TU 1277 (1). Reference specimens of *C. duodecimcostatus* from Italy: USNM 326663 (3) from Rio Torsero, Tuscany, Pliocene; USNM 156336 (3) from Alberga, Liguria, Pliocene; USNM 156310 (2) from Astigiano, Parona, Pliocene; USNM 155251 (2) from Coroncina, Pliocene.

Remarks.—The eight Dominican Republic specimens are referred to *C.* (*E.*) *duodecimcostatus* based on their corallum size and shape, number of septa, costal structure, and external resemblance to topotypic specimens of *C. duodecimcostatus* (Pl. 9, figs. 3–4). Unfortunately, calicular details are lacking in all specimens, making a certain identification impossible. Minor differences between the Dominican Republic specimens and the Italian specimens include the former having virtually straight coralla, whereas the Italian specimens have strongly-curved coralla. Also, the C1–2 of the Dominican Republic specimens are more prominent than those of the Italian specimens. However, Chevalier (1961) noted that this species was quite variable, particularly regarding the prominence of costae.

Comparisons.—Seven species of *Ceratotrochus* (*Edwardsotrochus*) were discussed by Chevalier (1961), all from the Miocene and Pliocene of Europe and northwest Africa. *C.* (*E.*) *duodecimcostatus* is distinguished by its hexameral symmetry, curved corallum, and by having up to five complete cycles of septa. No other species of this subgenus is known from the Caribbean Tertiary or Recent.

Occurrence.—Río Gurabo (Gurabo Formation) late Miocene (Text-fig. 3): loc. NMB 15836, loc. TU 1277. Río Mao (?Gurabo Formation): loc. TU 1225. "Yellow Shale" of Angostina (Duncan, 1864, p. 22).

Distribution of C. duodecimcostatus.—Miocene: northern Europe (Felix, 1927); ?late Miocene: Dominican Republic; Pliocene: southern Italy and northwest Africa (Chevalier, 1961; Felix, 1929); ?Neogene: Azores (Chevalier, 1964).

Genus **PARACYATHUS** Milne-Edwards and Haime, 1848b

Diagnosis.—Solitary; trochoid to turbinate; fixed. Septotheca costate. Paliform lobes often bilobed or trilobed, standing before all but last cycle of septa. Columella papillose, often indistinguishable from inner paliform lobes.

Type-species.—*Paracyathus procumbens* Milne-Edwards and Haime, 1848b, by subsequent designation (Milne-Edwards and Haime, 1850).

Distribution.—Eocene to Recent, cosmopolitan.

Paracyathus henekeni (Duncan, 1863)
Plate 8, figures 17, 18

Brachycyathus henekeni Duncan, 1863, pp. 426–428, pl. 15, fig. 1.
Paracyathus henekeni (Duncan). Duncan, 1868, pp. 16, 22, 27; Vaughan, 1919, pp. 213–214; Felix, 1927, p. 437; Frost and Langenheim, 1974, p. 302.
?*Paracyathus henekeni* (Duncan). Vaughan and Woodring, 1921, p. 152.

Description of lectotype [BM(NH) 28768].—Corallum conical (trochoid) and free; 5.1 mm in calicular diameter and 5.7 mm in height. Alternate costae thin and ridged, dentate near calice. Forty septa hexamerally arranged in four incomplete cycles: **S**1=**S**2>**S**3>**S**4. Fossa shallow. Paliform lobes slender but prominent teeth on septa of first three cycles. Columella papillose and small. Septal granules pointed, not carinate.

Diagnosis.—Costae straight, ridged, and dentate; calice round; paliform lobes discrete.

Type-material.—Eleven syntypes are deposited at the BM(NH), numbered 28768–28778. Because some of the specimens are not well preserved [*e.g.*, BM(NH) 28776, 28778], there is doubt about their identity, and therefore a lectotype is here designated: the figured specimen of Duncan (1863), BM(NH) 28768.

Type-locality.—"Nivaje Shale" of Heneken, Dominican Republic, Miocene.

Material.—BM(NH) 28768 (lectotype); BM(NH) 28769–28778 (paralectotypes).

Remarks.—No additional specimens of *P. henekeni* were collected and thus little can be added to Duncan's (1863) original description. We disagree, however, with Duncan's description of the paliform lobes as small, indistinct, and feebly-developed papillae. The paliform lobes are, in fact, discrete, prominent structures. Also, Duncan (1863) originally described the columella as large and papillose but later (Duncan, 1868) referred to it as small. We confirm his latter description.

Vaughan and Woodring's (1921) *P. henekeni* is not preserved well enough for identification.

Comparisons.—*Paracyathus henekeni* is compared to *P. sinuosus* in the following species account. It is unlike any other species of *Paracyathus* from the Caribbean or Tertiary of Europe.

Occurrence.—Known only from the type-locality in the Dominican Republic, Miocene.

Distribution.—Known only from the Miocene of the Dominican Republic.

Paracyathus sinuosus, new species
Plate 9, figures 5–9

Etymology.—The specific name *sinuosus* (Latin for "full of bendings") refers to the sinuous course of the costae on the upper theca.

Description.—Corallum ceratoid and straight, narrowing to a slender pedicel 1.5–1.9 mm in diameter. Pedicel expands basally up to 3 mm in diameter, forming the attachment. Calice of holotype (NMB D 5888) slightly elliptical, 4.5 × 4.1 mm in diameter; corallum 7.5 mm in height. Theca slightly porcelaneous, covered basally by beaded, equal costae. In upper half of corallum, costae ridged and often slightly sinuous (Pl. 9, fig. 8).

Septa hexamerally arranged in four cycles: **S**1>**S**2>**S**3>**S**4. **S**4 strongly fused to adjacent **S**3. This fusion, along with the **P**3, forms a large, solid structure in each half-system. Sides of septa and paliform lobes covered with prominent granules and carinae, the latter up to 0.1 mm in height and 0.3 mm long (Pl. 9, fig. 5).

Fossa shallow. Paliform lobes irregularly-shaped pillars occurring before first three cycles of septa. Columella papillose, composed of 10–15 irregularly-shaped rods similar in shape to paliform lobes but only about one-third the size and more deeply seated in fossa.

Diagnosis.—Corallum small; costae often sinuous; **S**4 fused to **S**3.

Type-material.—Holotype: NMB D 5888 from loc. NMB 15833. Paratypes: unnumbered NMB specimens from locs. NMB 15832 (8); 15833 (36); 17023 (1); 17024 (8); USNM 74686 (8) from loc. NMB 15833.

Type-locality.—Loc. NMB 15833: Río Gurabo (Mao Formation: 892 m above base of section), Dominican Republic, middle Miocene.

Reference material.—Nine specimens of *P. turonensis* from Pontlevoy, France (MNHNP L 61).

Remarks.—Vaughan and Woodring (1921, pp. 133, 163) listed three undetermined species of *Paracyathus* from the Miocene of the Dominican Republic: *Paracyathus* sp. (from loc. USGS 8540 and loc. USGS 8544), *Paracyathus* n. sp. a (from loc. USGS 8735 and loc. USGS 8591), and *Paracyathus* sp. b. (from loc. USGS 8591). Only specimens of the first two taxa have been located at the NMNH, and were judged to be inadequately preserved to identify as to genus.

Comparisons.—*Paracyathus sinuosus,* n. sp. is distinguished from *P. henekeni* (Duncan, 1863) by its shape, being ceratoid and attached instead of trochoid and free. Additionally, *P. sinuosus* can be distinguished by its sinuous costae and its inequality of **S**1 and **S**2.

It is distinguished from *Paracyathus,* n. sp. of Frost and Langenheim (1974) from the lower Miocene of Mexico by its smaller size, fewer septa, and differently-ornamented costae. Unfortunately, the Mexican species was based on only one poorly-preserved specimen.

Among the three European Miocene species of *Paracyathus* reported by Chevalier (1961), *P. sinuosus* is most similar to *P. turonensis* Milne-Edwards and Haime, 1848b. *P. turonensis,* however, has a broad

encrusting base, an almost cylindrical corallum, and broad, straight costae. Otherwise the calicular details are very similar.

The only Recent species known from the western Atlantic, *P. pulchellus* (Philippi, 1842), is easily distinguished by its greater corallum size, larger number of septa, and broader pedicel.

Occurrence.—Río Gurabo (Mao Formation) middle Pliocene (Text-fig. 3): locs. NMB 15832, 15833. Río Cana (Cercado Formation) lower Miocene (Text-fig. 3): locs. NMB 17023, 17024.

Distribution.—Known only from the late Miocene to middle Pliocene of the Dominican Republic from Río Gurabo and Río Cana.

Genus **DELTOCYATHUS**
Milne-Edwards and Haime, 1848b

Diagnosis.—Solitary; discoidal to patellate; free. Costae present. Pali before all but last cycle of septa; inner edges of **P**3 join adjacent **P**2 near columella, forming deltas. Columella papillose.

Type-species.—*Turbinolia italica* Michelotti, 1838, by monotypy.

Distribution.—Eocene to Recent, cosmopolitan.

Deltocyathus italicus (Michelotti, 1838)
Plate 9, figures 10–12

Turbinolia italica Michelotti, 1838, p. 51, pl. 1, fig. 8.
Deltocyathus italicus (Michelotti). Milne-Edwards and Haime, 1848b, pp. 326, pl. 10, fig. 11; Vaughan and Woodring, 1921, p. 147; Felix, 1927, pp. 440–441; Felix, 1929, p. 581; Chevalier, 1961, pp. 328–330 (synonymy); Chevalier, 1962, pp. 40–41.
?*Deltocyathus* sp. cf. *D. italicus* (Michelotti). Cairns, 1979, pp. 95–97, pl. 17, figs. 1–3.
?*Deltocyathus conicus* Zibrowius, 1980, pp. 83–85, pl. 39, figs. A–L.

*Description of Dominican Republic specimen (*USNM 63125 from loc. USGS 8702*).*—Corallum patellate: 7.6 mm in calicular diameter and 4.7 mm in height (basal angle 78°). Forty-eight costae: **C**1+2 equal in size, moderately ridged, and bear coarse granules. These 12 costae reach center of base. **C**3+4 progressively smaller and do not attain center of base.

Forty-eight hexamerally-arranged septa present but most calicular details are obscured by sediment. Only tips of some pali and columellar elements can be seen (Pl. 9, fig. 10).

Diagnosis.—Corallum conical (patellate), usually 10–11 mm in diameter; costae ridged, bearing coarse granules.

Type-material.—According to Chevalier (1961), Michelotti's holotype is lost.

Type-locality.—Tortona, Italy, Miocene (see Zibrowius, 1980, p. 85).

Material.—USNM 63125 (1) from loc. USGS 8702. Reference material of European *D. italicus* (Pl. 9, fig. 12): MNHNP L60 (2) from Tortona, Italy. Reference material of Caribbean Recent species (Cairns, 1979).

Remarks.—No additional specimens of *Deltocyathus* from the Caribbean Tertiary were examined; however, the specimen listed by Vaughan and Woodring (1921) was found in the collections of the NMNH (USNM 63125 from loc. USGS 8702), compared to typical European specimens, and found to be conspecific. However, the identity of the amphi-Atlantic Recent species (*D.* sp. cf. *D. italicus* (Michelotti) of Cairns, 1979 [see Pl. 9, fig. 13, herein] and *D. conicus* Zibrowius, 1980) is still a matter of debate. The major difference between the fossil and Recent forms is that the former has a coarser costal granulation, which led Zibrowius to describe a new species for the Recent specimens. The crux of the problem is that hundreds of Recent specimens are available for study, showing it to be variable in many characteristics (*i.e.,* corallum size, palar and columellar shape, and costal ornamentation), whereas there are relatively few Miocene specimens available for the study of variation. We therefore doubt whether *D. italicus* occurs in the Recent as well as the Neogene.

Comparisons.—No other fossil species of *Deltocyathus* are known from the Caribbean, and Chevalier (1961) reported only *D. italicus* from the Miocene of the western Mediterranean. There are, however, six Recent species known from the Caribbean (Cairns, 1979). *D. italicus* is distinguished from these by its strongly conical base and its ridged costae.

Occurrence.—Río Yaque del Norte (?Baitoa Formation) early Miocene: loc. USGS 8702.

Distribution.—Miocene: central and southern Europe (Felix, 1927; Chevalier, 1961), Morocco, ?Australia (see Zibrowius, 1980, p. 85), Dominican Republic; Pliocene: Modena, Italy (Felix, 1929); ?Recent: western Atlantic, 403–2634 m (Cairns, 1979) and eastern Atlantic, 1500–2300 m (Zibrowius, 1980 as *D. conicus*).

Subfamily **TURBINOLIINAE**
Milne-Edwards and Haime, 1848b

Genus **SPHENOTROCHUS**
Milne-Edwards and Haime, 1848b

Diagnosis.—Solitary and small; cuneiform; free. Costae long, prominent ridges or reduced to linear granules. Columella lamellar. Pali absent.

Subgenus **EUSTHENOTROCHUS** Wells, 1935

Diagnosis.—*Sphenotrochus* in which the costae have been reduced to rows of granules and/or short carinae.

Type-species.—*Sphenotrochus moseri* Wells, 1935 (= *S. gilchristi* Gardiner, 1904), by original designation.

Distribution.—Eocene to Recent of Europe, West Indies, and Indian Ocean.

Sphenotrochus (Eusthenotrochus) senni Wells, 1945
Plate 9, figures 14–19

Sphenotrochus n. sp. of Vaughan, 1919, p. 212; Vaughan and Hoffmeister, 1926, p. 114.
Sphenotrochus (*Eusthenotrochus*) *senni* Wells, 1945, p. 17, pl. 3, figs. 25, 34–35.
?*Sphenotrochus auritus* var. of Pourtalès. Lindström, 1877, pp. 11–12, pl. 2, figs. 21–22.

Description of Dominican Republic specimens.—Corallum cuneiform, highly compressed with a gently rounded base. Largest of three specimens 5.1 × 3.0 mm in calicular diameter and 7.0 mm in height. Five to seven costae on center of each lateral thecal face are continuous ridges, up to 1.9 mm long, occupying middle third of each thecal face. In upper third of corallum these costae become double rows of short carinae and granules 0.2–0.4 mm long. In lower third of corallum, approximately 1.8 mm above base, the longitudinally-ridged costae become slightly constricted (Pl. 9, fig. 16) and re-radiate basally into short ridges. All other costae (*i.e.*, those on either side of the elongate costae) composed of short carinae and granules, much like those of distal third of ridged costae. Commonly two rows of granules per septum near calicular edge.

Septa hexamerally-arranged in three cycles: **S1=S2>S3**. Six of the 12 large septa, those originating from lateral faces, reach lamellar columella.

Diagnostic characters.—Distinctive costal morphology, composed of ridges in center third of lateral faces and a linear arrangement of granules for upper and lower third of faces.

Type-material.—USNM 68358 (holotype): Height = 8.9 mm, calicular diameter = 6.2 × 4.4 mm.

Type-locality.—Martinique, Bassignac tuffs, middle Miocene.

Material.—Two unnumbered specimens from loc. NMB 15900; NMB D 5891 (1) from loc. NMB 16938; USNM 68358 (holotype). Reference material: USNM 68407, *Sphenotrochus* n. sp. of Vaughan (1919); ?*S. auritus* var. Pourtalès of Lindström (1877), Naturhistoriska Riksmuseet, Stockholm, specimen 120.

Remarks.—The Dominican Republic specimens differ slightly from the type specimen in having several distinctly-ridged costae on the middle third of each lateral thecal face. The holotype has only one elongate costa 1.2 mm long on one face.

Wells (1945) reported three rows of granules per septum at the calicular edge. The Dominican Republic specimens have only two rows of granules per septum and a reevaluation of the holotype shows this character to be equivocal because of poor preservation.

Comparisons.—*Sphenotrochus* (*E.*) *senni* is similar to *S.* (*E.*) *brassensis* Vaughan *in* Vaughan and Hoffmeister, 1925, the latter known from the middle Miocene of Trinidad. Unfortunately, the type and only known specimen of *S. brassensis* is too small and damaged to allow a proper comparison.

The specimens reported by Lindström (1877) as *Sphenotrochus auritus* var. Pourtalès from the Recent of the Virgin Islands are also very similar to *S. senni,* particularly in corallum shape and costal ornamentation. Lindström's specimens are not *S. auritus* Pourtalès, 1874, but, instead, represent either a new species or *S.* (*E.*) *senni* in the Recent.

The unidentified *Sphenotrochus* specimen alluded to by Vaughan (1919), Vaughan and Hoffmeister (1926), and Wells (1945) from the Bowden Formation of Jamaica (USNM 68407) was reexamined and is considered to be *S.* (*E.*) *senni.*

Occurrence.—Río Gurabo (Cercado Formation) late Miocene (Text-fig. 3): loc. NMB 15900. Río Yaque del Norte (?Baitoa Formation) early Miocene: loc. NMB 16936.

Distribution.—Miocene: Martinique, Dominican Republic; late Pliocene: Jamaica (Vaughan, 1919); ?Recent: Virgin Islands (Lindström, 1877 as *S. auritus* var. Pourtalès).

Genus **DOMINICOTROCHUS** Wells, 1937

Diagnosis.—Solitary; cuneiform; free. Septotheca costate; principal costae alate. Lacking columella, pali, and endotheca.

Type-species.—*Smilotrochus dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925.

Distribution.—Miocene of West Indies.

Dominicotrochus dominicensis (Vaughan, 1925)
Plate 9, figures 20, 21

Smilotrochus ? *dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925, p. 316, pl. 1, figs. 1–2; Felix, 1927, p. 401.
Dominocotrochus dominicensis (Vaughan). Wells, 1937, p. 14; Wells, 1945, pp. 17–18, pl. 3, figs. 26–33; Wells, 1956, p. F426; ?Frost and Langenheim, 1974, p. 304, pl. 117, figs. 5–8.

Diagnosis.—Corallum cuneiform and free, with alate lateral edge costae. Coralla up to 6.5 × 10.0 mm in calicular diameter and 13 mm in height. Costae distinct. Septa hexamerally arranged in five incomplete cycles: **S1=S2**. Fossa deep.

Type-material.—MCZ 9266 (holotype) missing from the MCZ.

Type-locality.—Dominican Republic, without specific locality, ?Miocene.

Material.—Eight specimens from Martinique reported by Wells (1945): USNM 68359.

Remarks.—Frost and Langenheim (1974) reported *D. dominicensis* from the lower Miocene of Mexico. Although we did not examine these three specimens, we query their identification based on the apparent poor preservation of the specimens as illustrated and described.

Comparisons.—*Dominicotrochus* is a monotypic genus within the Turbinoliinae characterized by lacking a columella.

Occurrence.—The single record known from the Dominican Republic (the holotype), was reported without specific locality.

Distribution.—?Lower Miocene: Mexico (Frost and Langenheim, 1974); middle Miocene: Martinique (Wells, 1945); Miocene: Dominican Republic.

Subfamily **PARASMILIINAE** Vaughan and Wells, 1943

Genus **ASTEROSMILIA** Duncan, 1867

Diagnosis.—Solitary; ceratoid, trochoid, or flabellate; free or attached. Paliform lobes before penultimate and sometimes antepenultimate cycle of septa. Columella lamellar or fascicular. Endotheca abundant.

Type-species.—*Trochocyathus abnormalis* Duncan, 1864, by subsequent designation (Vaughan, 1919).

Remarks.—The species of *Asterosmilia* discussed here are ordered as follows: the type species, followed by the other species found in order of decreasing similarity to the type species.

Distribution.—Oligocene to Recent of West Indies.

Asterosmilia abnormalis (Duncan, 1864)
Plate 10, figures 1–4, 6

Trochocyathus abnormalis Duncan, 1864, p. 26, pl. 2, figs. 4a–c.
Asterosmilia anomala (Duncan) [*sic*]. Duncan, 1867, p. 653, pl. 32, figs. 3a–d; Duncan, 1868, pp. 16, 23; Pourtalès, 1875, p. 545.
Asterosmilia cornuta Duncan, 1867, p. 653, pl. 32, fig. 4; Duncan, 1868, pp. 16, 23; Vaughan, 1919, pp. 213, 354.
Asterosmilia coronata Duncan. Pourtalès, 1875, p. 545.
Asterosmilia abnormalis (Duncan). Vaughan, 1919, pp. 213, 354; Vaughan and Woodring, 1921, p. 133; Vaughan and Hoffmeister, 1925, p. 322; Felix, 1927, p. 312; Frost and Langenheim, 1974, p. 305.

Description.—Corallum ceratoid, slender, and curved 10°–100° in plane of greater calicular axis. Corallum compressed, the compression most apparent in basal part. Largest corallum examined (USNM 546428 from loc. USGS 8516) 46 mm in height; largest calice (in largest corallum), 18.7 × 14.8 mm in diameter. Theca light reddish-brown. Pedicel very narrow, 1.0–1.3 mm in diameter. **C**1+2 prominent, the **C**1 on convex thecal edge often forming a crest up to 2 mm in height and 10 mm long on basal one-third to one-fourth of larger coralla. Less frequently the opposing **C**1 on concave thecal edge is also ridged. **C**3–5 low and smooth.

Septa hexamerally arranged in five incomplete cycles. **S**1+2 equal in size and moderately exsert. Higher cycle septa progressively smaller and less exsert. Largest corallum has 72 septa.

According to Duncan (1864), paliform lobes occur before all but last cycle of septa; however, none of the specimens available to us are preserved well enough to confirm this observation. Columella commonly lamellar but may be spongy. Lower half of corallum solidly filled with stereome. Upper half filled with obliquely-oriented dissepiments.

Diagnostic characters.—Well-developed, alate costa on convex thecal edge; paliform lobes before **S**1–3.

Type-material.—Duncan (1864) did not specify how many specimens formed the base of his description of *A. abnormalis,* only that he had two or more. Six specimens referable to this species are deposited at the BM(NH) [BM(NH) 28801–28806], all of which are considered as syntypes. Duncan's (1864, pl. 2, fig. 4) illustrated specimen is BM(NH) 28801.

The holotype of *A. cornuta* is also deposited at the BM(NH) [BM(NH) 28807].

Type-locality.—The type-locality of both *A. abnormalis* and *A. cornuta* is the "Nivaje Shale" of Heneken, Dominican Republic, Miocene.

Material.—Unnumbered NMB specimens from locs. NMB 15806 (1); 15814 (1); 16868 (1); 16910 (19); USNM 546428 (73) from loc. USGS 8516; USNM 546427 (44) from loc. USGS 8519; unnumbered TU specimens from loc. TU 1219 (35); loc. TU 1380 (8); loc. TU 1411 (1); BM(NH) 28801–28806 (syntypes of *A. abnormalis*); BM(NH) 28807 (holotype of *A. cornuta*). Reference material: USNM 65323 (1) from loc. USGS 8321 (Costa Rica).

Remarks.—Ordinarily the columella type is a conservative character at the species level and even often at the generic level; however, the columella of *A. abnormalis* may be either lamellar or spongy. A similar kind of variation was noted by Cairns (1979) for the Recent species *A. prolifera* (Pourtalès, 1871) [see Pl. 10, fig. 5 herein]. In an examination of over 1800 specimens of *A. prolifera,* Cairns found extreme variation in columellar and palar shape; in rare cases columella and pali were missing. This range of variation found in a congener gives support to identifying specimens that have either a lamellar or spongy columella as *A. abnormalis.*

The lateral-edge costal crests of Duncan's illustrated specimen (1864, pl. 2, fig. 4a) are grossly exaggerated. There is, in fact, no costal ridge on the concave thecal edge, and the convex edge crest is much smaller than illustrated (Pl. 10, figs. 2–3).

Comparisons.—The long, curving ceratoid corallum with an alate costa on the convex thecal edge distinguishes *A. abnormalis* from the other nine species of

Table 3.—Characters of the 10 known species of *Asterosmilia*.

	corallum shape and size	*nature of costae*	*pedicel diameter*	*septal cycles*[5]
A. abnormalis (Duncan, 1864)	ceratoid, curved; medium	lateral costae alate (esp. concave side)	narrow	**S**4+
A. exarata Duncan, 1867	ceratoid, curved; small	**C**1+2>**C**3+4	narrow	**S**4
A. marchadi (Chevalier, 1966)	ceratoid; small	**C**1+2>**C**3+4	narrow	**S**4+
A. profunda (Duncan, 1864)	trochoid, curved; large	**C**1+2 slightly ridged	thick	**S**5
A. duncani[1] Vaughan *in* Vaughan and Hoffmeister, 1925	calice constricted in center, straight; medium	equal, all slightly ridged	narrow	**S**5+
A. compressa[2] Vaughan *in* Vaughan and Hoffmeister, 1925	flabellate, straight; medium	alate edge costae	narrow	**S**5+
A. machapooriensis Hoffmeister *in* Vaughan and Hoffmeister, 1926	ceratoid, curved; medium	**C**1–3 slightly ridged	narrow	**S**4+
A. trinitatis[3] Vaughan *in* Vaughan and Hoffmeister, 1926	flabellate, straight; medium	alate edge costae	thick	**S**4+
A. pourtalesi[4] Duncan, 1873	ceratoid to sub-cylindrical, curved; medium	**C**1–3>**C**4	unknown	**S**4+
A. prolifera (Pourtalès, 1871)	ceratoid to trochoid, curved; small to medium	equal, low	narrow	**S**4+

[1] Based only on the holotype; [2] Based only on the four syntypes; [3] Based on few poorly preserved specimens (the types). Generic attribution doubtful; [4] Not seen; [5] A plus sign means an incomplete cycle of the next higher numbered septal cycle.

Asterosmilia (Table 3). It is morphologically very similar to *A. prolifera,* particularly with regard to corallum size and shape. *A. prolifera* differs in having equal and nonalate costae, dissepiments extending to the base of long coralla, and a less compressed corallum.

Occurrence.—Río Gurabo (Gurabo Formation) late Miocene to early Pliocene (Text-fig. 3): locs. NMB 15806, 15814. Río Cana (Gurabo Formation) early Pliocene (Text-fig. 3): loc. NMB 16868. Río Mao (?Gurabo Formation) late Miocene: loc. NMB 16910, loc. USGS 8519. Río Amina: loc. USGS 8516, loc. TU 1219. "Nivaje Shale", South of Santiago de los Caballeros (?Gurabo Formation): loc. TU 1380. Río Guanajuma (?Gurabo Formation): loc. TU 1411.

Distribution.—Known only from the late Miocene to early Pliocene of the Dominican Republic from Río Gurabo, Río Mao, Río Amina, "Nivaje Shale", and Río Guanajuma.

Asterosmilia exarata Duncan, 1867
Plate 10, figures 7–9, 11

Asterosmilia exarata Duncan, 1867, p. 653, pl. 32, fig. 5; Duncan, 1868, pp. 16, 23; Pourtalès, 1875, p. 545; Vaughan, 1919, pp. 213, 354; Vaughan and Hoffmeister, 1925, p. 322; Felix, 1927, p. 312.

Asterosmilia hilli Vaughan, 1919, pp. 212, 228–229, 355–356, pl. 80, figs. 4–6; Vaughan and Woodring, 1921, pp. 99, 133; Vaughan and Hoffmeister, 1925, p. 322; ?Felix, 1927, p. 213; ?Frost and Langenheim, 1974, pp. 304–305, pl. 117, figs. 1–2.

?*Asterosmilia exarata* var. Vaughan, 1919, pp. 200, 218.

Not *Asterosmilia exarata* Duncan. Vaughan and Woodring, 1921, p. 133 (= *A. profunda* and an unidentified species of *Asterosmilia*).

?*Asterosmilia exarata* var. *robusta* Vaughan and Hoffmeister, 1925, p. 324; Felix, 1927, p. 312.

?*Asterosmilia* sp. cf. *A. hilli* Vaughan. Wells, 1934, p. 106.

Description.—Corallum ceratoid, slender, and curved 45°–90° in plane of greater calicular axis. Corallum slightly compressed, almost round in cross-section. Holotype [BM(NH) 28944], one of the largest coralla of this species examined, 18.1 mm in height and 9.6 × 8.8 mm in calicular diameter. Pedicel narrow, about 1.4 mm in diameter. **C**1–2 slightly more prominent than **C**3–4, but all costae distinct, convex, granulated ridges. No alate costae.

Septa hexamerally arranged in four cycles, the fourth cycle complete at a **gcd** of about 9.5 mm. **S**1+2 equal in size and exsertness, the higher cycle septa progressively smaller. A prominent paliform lobe occurs before each **S**3, forming a crown of 12 elements in large, well-preserved specimens. Paliform lobes broad (about 1.45 mm wide) and separated from their adjacent **S**3 by a deep and wide notch. Columella usually lamellar, often with two or three deep indentations; however, some specimens have trabecular columellas, showing the same variation found in *A. abnormalis* and *A. prolifera.* Endothecal dissepiments present (Pl. 10, fig. 11) but sparse.

Diagnostic characters.—Corallum small; never more than four cycles of septa.

Type-material.—BM(NH) 28944 (holotype of *A. exarata*); USNM 324815 (7 syntypes of *A. hilli*); USNM 324816 (3 syntypes of *A. hilli*).

Type-locality.—*A. exarata*: "Nivaje Shale", Dominican Republic, Miocene. *A. hilli*: loc. USGS 2580, Jamaica (Bowden Formation) late Pliocene.

Material.—USNM 546422 (17) from loc. USGS 8446; USNM 546411 (7) from loc. USGS 8733; USNM 324815 (7 syntypes of *A. hilli*); USNM 324816 (3 syntypes of *A. hilli*); BM(NH) 28944 (holotype of *A. ex-*

Table 3.—Continued.

paliform lobe cycles	*nature of columella*	*endothecal dissepiments*	*distribution and age*
P1–3?	lamellar and spongy	abundant, oblique, stereome present	Dominican Republic (late Miocene to early Pliocene)
P3	lamellar and trabecular	sparse	?Barbados (Eocene) ?Antigua (late Oligocene) ?Mexico (Miocene) Costa Rica, Dominican Republic (Miocene) Jamaica (Pliocene) Atlantic (Recent: 32–229 m)
P3	crispate	abundant	Jamaica (Miocene)
P3+4	lamellar and fascicular	abundant, no stereome	Dominican Republic (late Miocene to middle Pliocene)
P4?	linear–papillose	abundant, stereome present	Dominican Republic (?Miocene)
P4	lamellar	sparse	Dominican Republic (?Miocene)
P1–2	spongy	abundant	Trinidad (Miocene)
P3 or **P**4	lamellar	sparse	Trinidad (Miocene)
?	lamellar	present	St. Barthelemy (Oligocene)
P3	papillose and lamellar	abundant, stereome present	Atlantic (Recent: 32–311 m)

arata); USNM 44303 [*A.* sp. cf. *A. hilli* of Wells (1934)]. Reference specimens: USNM 63329 (43) from loc. USGS 2580 (Jamaica); USNM 63129 (14) from loc. USGS 20468 (Costa Rica); USNM 324814 (14) from Limon, Costa Rica, Pittier #618; USNM 63611 (1) [*A. exarata* var. "*robusta*"] from loc. USGS 6881 (upper Oligocene, Antigua).

Remarks.—The specimen reported by Wells (1934) as *Asterosmilia* sp. cf. *A. hilli* from the Eocene of Barbados (Pl. 10, fig. 10) is a poorly-preserved fragment missing its calicular features. Its size and costae are consistent with *A. exarata,* but a definitive identification is impossible.

The single, poorly-preserved, immature specimen of *A. hilli* reported by Frost and Langenheim (1974) from the lower Miocene of Mexico is also highly suspect on the basis of its poor preservation and the presence of an epitheca; however, this specimen was not examined by either author.

Vaughan and Hoffmeister (1925) alluded to a variety of *A. exarata* that Vaughan called *robusta,* but that variety was never described or figured and therefore must be considered a *nomen nudum.* This is undoubtedly the unnamed variety of *A. exarata* referred to by Vaughan (1919, pp. 200, 218) from Antigua and the Dominican Republic. According to Vaughan and Hoffmeister (1925), the form occurred together with *A. duncani* Vaughan, 1925 in the blue clay of the Dominican Republic. A specimen labelled as such in Vaughan's handwriting is deposited at the NMNH (USNM 63611, from loc. USGS 6811, Willoughby Bay, Antigua). It is not conspecific with *A. exarata* and is too poorly preserved to properly identify. No specimen of variety *robusta* was found in the NMNH collections from the Dominican Republic.

Comparisons.—*Asterosmilia exarata* is extremely similar to the Recent species *A. marchadi* (Chevalier, 1966) (Table 3). The only differences noted are that *A. exarata* sometimes has a lamellar columella and has equal-sized **S**1+2, whereas *A. marchadi* has a crispate columella and its **S**1 are distinctly larger than its **S**2.

A poorly-preserved specimen, especially one lacking calicular details, could easily be confused with *Trochocyathus chevalieri,* n. sp., based on similarity of size, shape, number of septa and costae. Nonetheless, on closer examination one would find that *T. chevalieri* has twice as many pali (**P**1+2 as well as **P**3), a papillose columella, and no endothecal dissepiments.

Occurrence.—Río Mao (?Cercado Formation) late Miocene: loc. USGS 8733. Río Gurabo: loc. USGS 8446.

Distribution.—?Eocene: Barbados (Wells, 1934, as *A. hilli*); ?upper Oligocene: Antigua (Vaughan, 1919, pp. 200, 218 as *A. exarata* var.); ?early Miocene: Mexico (Frost and Langenheim, 1974); Miocene: Costa Rica (Vaughan, 1919, as *A. hilli*); late Miocene: Dominican Republic; late Pliocene: Jamaica (Vaughan, 1919, as *A. hilli*).

Asterosmilia profunda (Duncan, 1864)
Plate 10, figures 12–18

Trochocyathus profundus Duncan, 1864, p. 26, pl. 5, figs. 3a–c.
Asterosmilia exarata Duncan. Vaughan and Woodring, 1921, p. 133 (in part: USNM 546415, 546416, 546417, 546424).
Asterosmilia profunda (Duncan). ?Vaughan and Woodring, 1921, pp. 99, 133; Vaughan and Hoffmeister, 1925, p. 322; Vaughan and Hoffmeister, 1926, p. 117; Felix, 1927, pp. 312–313.

Description.—Corallum trochoid, massive, and often irregularly curved in basal region. Largest corallum examined (USNM 63327 from loc. USGS 2580) 90.0

mm long and 27 × 22 mm in calicular diameter. Theca light reddish-brown. Pedicel thick, sometimes attached to substrate, 3.3–5.8 mm in diameter. C1–2 often slightly ridged but no alate costae present. C3–5 flat and equal in width, covered by small granules. Theca smooth and sometimes porcelaneous.

Septa hexamerally arranged in five cycles: S1=S2>S3>S4>S5. Fifth cycle usually complete at a **gcd** of about 25 mm.

Paliform lobes before penultimate (S4) and antepenultimate (S3) cycles of septa. As in most other species of *Asterosmilia,* the columella is variable: either fascicular (*e.g.,* Bowden specimens) or lamellar (*e.g.,* most of the Dominican Republic specimens). Fossa deep. Vesicular dissepiments abundant, extending to base of corallum.

Diagnostic characters.—Large, robust, trochoid corallum; thick, attached pedicel.

Type-material.—BM(NH) 40413 (holotype): height = 38.8 mm, 25.7 × 19.8 mm in calicular diameter.

Type-locality.—Jamaican "Miocene".

Material.—Unnumbered NMB specimens from locs. NMB 15832 (1); 15833 (7); USNM 546417 (3) from loc. USGS 8527; USNM 546424 (2) from loc. USGS 8528; USNM 546415 (1) from loc. USGS 8556; USNM 546416 (3) from loc. USGS 8733; unnumbered TU specimens from loc. TU 1208 (2); loc. TU 1225 (7); loc. TU 1352 (14); loc. TU 1366 (1); loc. TU 1451 (2); loc. TU 1453 (1); BM(NH) 40413 (holotype of *T. profundus*). Reference specimens: USNM 63327 (10) from loc. USGS 2580 (Jamaica); USNM 64213 (3) from loc. USGS 8421, Eocene of Panama.

Remarks.—The specimen reported by Vaughan and Woodring (1921, p. 133) as *A. profunda* from loc. USGS 8733 is present at the NMNH (USNM 546412) but is too small to identify. Other specimens from the same station identified by Vaughan and Woodring (1921, p. 133) as *A. exarata* Duncan, 1867 are *A. profunda.*

Comparisons.—The massive trochoid corallum and relatively thick pedicel serve to distinguish *A. profunda* from its congeners. Although Vaughan and Hoffmeister (1926) compared it to *A. machapooriensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926, we feel that, of all the species of *Asterosmilia,* it most resembles *A. duncani* Vaughan, 1925, but can be distinguished by a number of characters (Table 3).

Occurrence.—Río Gurabo (Mao and Gurabo formations) early to middle Pliocene (Text-fig. 3): locs. NMB 15832, 15833, locs. USGS 8550, 8556, locs. TU 1352, 1366. Río Mao (?Gurabo Formation) late Miocene: locs. USGS 8527, 8528, 8733, loc. TU 1453. "Nivaje Shale". Arroyo Babosico (?Gurabo Formation): loc. TU 1451.

Distribution.—Eocene: Panama (reported herein); Miocene: Jamaica (Duncan, 1864); late Miocene to middle Pliocene: Dominican Republic.

Asterosmilia duncani Vaughan, 1925
Plate 10, figures 19, 20

Asterosmilia n. sp. of Vaughan, 1919, p. 354 (one of two "additional species").

Asterosmilia duncani Vaughan *in* Vaughan and Hoffmeister, 1925, pp. 323–324, pl. 3, figs. 1–2; Felix, 1927, p. 312.

Description based on holotype (MCZ 9277).—Corallum compressed, straight, and free; 26.1 × 19.0 mm in calicular diameter and 33.5 mm in height. Calice slightly constricted in center, about 18 mm in **lcd**. Lateral calicular edges rounded; no alate costae. Costae thin and ridged. Ninety-two costae and septa present but more detailed observations of symmetry and number of cycles not possible because of poor preservation. According to Vaughan and Hoffmeister (1925), paliform lobes present before penultimate septal cycle (usually S4). Columella well developed, composed of a row of interconnected papillae. Dissepiments abundant; stereome in base of corallum.

Type-material.—MCZ 9277 (holotype).

Type-locality.—Dominican Republic (Gabb Collection), ?lower Miocene.

Material.—We have examined the holotype (MCZ 9277), which is the only known specimen of this species.

Remarks.—There was no evidence of paliform lobes in the holotype.

Comparisons.—*Asterosmilia duncani* is distinguished from other species of *Asterosmilia* by its compressed corallum (constricted in center) and relatively high number of septa. However, comparisons based on a single damaged specimen are inadequate.

Occurrence.—Known only from the type-locality of "Dominican Republic", ?lower Miocene.

Distribution.—Known only from the ?lower Miocene of the Dominican Republic.

Asterosmilia compressa Vaughan, 1925
Plate 10, figures 21–24

Asterosmilia n. sp. of Vaughan, 1919, p. 354 (one of two "additional species").

Asterosmilia compressa Vaughan *in* Vaughan and Hoffmeister, 1925, pp. 322–323, pl. 3, figs. 3–4; Vaughan and Hoffmeister, 1926, p. 117; Felix, 1927, p. 312.

Diagnosis based on the syntypes.—Corallum strongly compressed, straight, and free. Pedicel 2–3 mm in diameter. Largest of four syntypes (specimen 4 of Vaughan and Hoffmeister, 1925) 10.8 × 25.3 mm in calicular diameter and 35.4 mm in height. Costae low and distinct, every fourth costa (*i.e.,* C1–3) slightly more prominent; two principal costae alate. Septa hexamerally arranged in five complete cycles plus pairs of

S6 even at a **gcd** of 20 mm; largest specimen with 135 septa. Small paliform lobes before penultimate septal cycle (usually S4). Columella lamellar. Dissepiments sparse.

Type-material.—MCZ 9273–9276 (four syntypes).

Type-locality.—Dominican Republic (Gabb Collection), ?lower Miocene.

Material.—We have examined the four syntypes (MCZ 9273–9276); no additional specimens are known of this species.

Comparisons.—*Asterosmilia compressa* is similar to *A. trinitatis* Vaughan *in* Vaughan and Hoffmeister, 1926, in size, shape, and costal morphology, as previously noted by Vaughan and Hoffmeister (1926). It is distinguished by having a narrower pedicel and a greater number of septa at a corresponding **gcd** (Table 3).

Occurrence.—Known only from the type-locality of "Dominican Republic", lower Miocene.

Distribution.—Known only from the ?lower Miocene of the Dominican Republic.

Superfamily **FLABELLICAE** Bourne, 1905

Family **FLABELLIDAE** Bourne, 1905

Genus **FLABELLUM** Lesson, 1831

Diagnosis.—Solitary; cuneiform, compressed-turbinate, or ceratoid; free. Wall epithecal. Base not thickened by stereome; roots absent. Pali absent. Columella rudimentary or absent.

Type-species.—*Flabellum pavoninum* Lesson, 1831, by monotypy.

Distribution.—Eocene to Recent, cosmopolitan.

?Flabellum species
Plate 11, figures 1, 2

Flabellum b Vaughan and Woodring, 1921, p. 133.

Diagnosis.—Corallum flabellate, largest specimen (USNM 64202 from loc. USGS 8733) 20.8 × 13.9 mm in calicular diameter, 29.1 mm in height, and 1.5 mm in pedicel diameter. C1–2 highly ridged, especially two principal costae, which project up to 4 mm. C1 extend to pedicel; C2 about three-quarters that distance. Corallum epithecate, covered by transverse epithecal bands. Septa hexamerally arranged in four cycles; some pairs of S5 in lateral edge half-systems. Details of septa and fossa not preserved.

Material.—USNM 64202 (2) from loc. USGS 8733; 2 unnumbered TU specimens from loc. TU 1225. Reference material: USNM 155290 and 155288 (8), *F. roissyanum* Milne-Edwards and Haime, 1848b from Miocene of Austria.

Remarks.—This taxon is quite different from any other species described from the Dominican Republic but because its preservation does not allow an examination of the calicular details, the generic attribution is tentative.

Five species of *Flabellum* have been reported from the Dominican Republic: *F. dubium* Duncan, 1863; *F. exaratum* Duncan and Wall, 1865 (by Duncan, 1868, p. 16); *Flabellum,* n. sp. *sensu* Duncan (1863, pp. 411, 430); and *Flabellum* a and b *sensu* Vaughan and Woodring (1921). *Flabellum dubium* was transferred to *Antillophyllia* Vaughan, 1932 by Vaughan (1932, p. 509). After examination of the type of *F. exaratum,* we concur with Vaughan (1919, p. 213) that the specimen does not belong to *Flabellum,* but probably to a group of species ascribed to the genus *Placocyathus* (see discussion of *Antillocyathus*). *Flabellum,* n. sp. of Duncan (1863) was based on casts that do not allow a definitive determination. *Flabellum* a of Vaughan and Woodring (1921) was determined to be *Pourtalocyathus hispidus* (Pourtalès, 1878) [this paper]. Finally, Vaughan and Woodring's *Flabellum* b, the specimen figured and diagnosed in this account, is also of doubtful generic identity. Thus, of the five records, no species of *Flabellum* are definitely known to occur in the Dominican Republic.

In corallum shape and costal characteristics the four Dominican Republic specimens resemble *F. roissyanum,* known from the Miocene to Pliocene of southern Europe (see Kojumdgieva and Strachimirov, 1960).

Occurrence.—Río Mao (?Gurabo Formation) late Miocene: loc. USGS 8733. Río Mao (?Gurabo Formation): loc. TU 1225.

Family **GUYNIIDAE** Hickson, 1910

Genus **POURTALOCYATHUS** Cairns, 1979

Diagnosis.—Solitary and small; ceratoid; free. Wall epithecal, often with one row of mural spots (differential calcification) in every interseptal space. Three cycles of septa; small paliform lobes before S2. Columella papillose.

Type-species.—*Ceratotrochus hispidus* Pourtalès, 1878, by original designation.

Distribution.—Miocene to Recent, West Indies.

Pourtalocyathus hispidus (Pourtalès, 1878)
Plate 11, figures 3–7, 10–11

Ceratotrochus hispidus Pourtalès, 1878, p. 202, pl. 1, figs. 19–20.
Flabellum a of Vaughan and Woodring, 1921, p. 133.
Pourtalocyathus hispidus (Pourtalès). Cairns, 1979, pp. 171–172, pl. 33, figs. 3–8 (includes synonymy).

Description.—Corallum ceratoid, straight to slightly curved, and small. Typical corallum 8–9 mm in height and about 4.2 mm in calicular diameter; calice round. Coralla often attached by a relatively thick pedicel about 1.2 mm in diameter; base of pedicel reveals six primary

septa. Costae equal, slightly convex, and smooth. Fine concentric epithecal bands encircle the theca. In some coralla, rows of round to elongate mural pores about 0.25 mm in diameter occur in every interseptal space (Pl. 11, figs. 10, 11).

Septa hexamerally arranged in three complete cycles (24 septa). **S**1 highly exsert and very thick (up to 0.26 mm). **S**2–3 much less exsert and progressively smaller in size and thickness (about 0.07 mm thick). Only **S**1 reach columella. Granules up to 68 μm in height (Pl. 11, fig. 6) occur on all septal faces.

Fossa shallow. Small, papillose paliform lobes often before **S**2. Columella well-developed and papillose, composed of several solid, basally-fused rods.

Diagnostic characters.—Mural spots or pores often present; three cycles of septa; **S**1 very exsert; corallum small, rarely over 5 mm in calicular diameter.

Type-material.—MCZ 5583 (holotype).

Type-locality.—U. S. Coast Survey Steamer *Blake* sta. 19: 23°02′N, 83°10′W (western Straits of Florida), 567 m; Recent.

Material.—Unnumbered NMB specimens from locs. NMB 15823 (10); 15828 (19); 15829 (3); 15995 (2); 16016 (4); 16023 (1); 16036 (8); 16038 (4); USNM 63040 (2) from loc. USGS 8726; USNM 64200 (2) from loc. USGS 8733; USNM 64201 (5) from loc. USGS 8735; 89 unnumbered TU specimens from loc. TU 1227A; MCZ 5583 (holotype). Reference material: 123 Recent specimens listed by Cairns (1979).

Remarks.—The rows of white mural spots corresponding to each interseptal space, reported by Cairns (1979) for about one-third of the Recent specimens, are also found in the Dominican Republic fossils with about the same frequency. These spots, which when the specimen is alive have no surface relief, probably represent a periodic differential calcification of the theca because in many of the fossil specimens these spots are now pores penetratng the theca.

Some Recent specimens have granulated costae, hispid spines, or imbricate epithecal bands. Dominican Republic specimens have consistently smooth epitheca.

This is the first fossil record of *P. hispidus.* The Dominican Republic Miocene fossils are indistinguishable from Recent specimens.

Comparisons.—*Pourtalocyathus* is a monotypic genus within the Guyniidae characterized by its papillose columella, large **P**2, and three cycles of septa.

Occurrence.—Río Gurabo (Mao Formation) early to middle Pliocene (Text-fig. 3): locs. NMB 15823, 15828, 15829, 15995, 16016, 16023, 16036, 16038, loc. USGS 8735. Río Mao (?Gurabo Formation) late Miocene: loc. USGS 8733. Río Yaque del Norte (?Baitoa Formation) loc. USGS 8726. Arroyo Zalaya (?Gurabo Formation): loc. TU 1227A.

Distribution.—Late Miocene to middle Pliocene: Dominican Republic; Recent: Antilles and off eastern Florida, 349–1200 m (Cairns, 1979).

Genus **GUYNIA** Duncan, 1872

Diagnosis.—Solitary; ceratoid to cylindrical; free or laterally attached. Wall epithecal, often with rows of mural pores between septa. Pali absent. Columella composed of one twisted ribbon.

Type-species.—*Guynia annulata* Duncan, 1872, by monotypy.

Distribution.—Eocene to Recent, cosmopolitan.

Guynia species cf. **G. annulata** Duncan, 1872
Plate 11, figures 8, 9, 12, 13

Guynia annulata Duncan, 1872, p. 32, pl. 1, figs. 1–8; Wells, 1973, pp. 59–63, figs. 1–3; Cairns, 1979, pp. 164–165, pl. 32, figs. 1–3 (synonymy); Zibrowius, 1980, pp. 161–163, pl. 83, figs. A–Q; Cairns, 1984, p. 23, pl. 5, figs. A–B.

Pyrophyllia inflata Hickson, 1910, pp. 1–7, text-figs. 1–4.

Description of Dominican Republic specimens.—Corallum straight and cylindrical; largest specimen (unnumbered TU specimen from loc. TU 1227A) 3.25 mm long and 0.9 mm in calicular diameter. Coralla show no sign of lateral attachment. Concentric epithecal growth bands occur about every 0.12–0.15 mm. Longitudinal costae (**C**1) also present. Prominent spines up to 0.10 mm in height occur at the intersections of costae and epithecal bands. In two specimens mural pores about 0.10 mm in diameter are present.

Eight **S**1. Inner septal edges very sinuous; septal faces smooth. **S**2, if present, are much lower in fossa than **S**1 and therefore obscured from view. Columella also obscured.

Diagnostic characters.—Very small corallum; octameral symmetry; two septal cycles; no septal granules.

Type-material.—BM(NH) 1883.12.10.110–112 (18 syntypes).

Type-locality.—Adventure Bank, Mediterranean, 168 m, Recent.

Material.—Two unnumbered TU specimens from loc. TU 1227A; USNM 74689 (1) from loc. TU 1227A. Reference material: Recent specimens from the western Atlantic and Hawaii (Cairns, 1979, 1984); BM(NH) 1883.12.10.110–112 (18 syntypes of *G. annulata*).

Remarks.—The Dominican Republic specimens differ from Recent specimens in having spines at the intersections of the costae and epithecal bands. But, given the range of variation of the theca described by

Cairns (1979, p. 164), this is not considered to be a differentiating character.

Comparisons.—Only one other species of *Guynia* is known: *G. adherens* (Tenison-Woods, 1878) from the Oligocene of Aldinga, Australia. It differs from *G. annulata* in having three cycles of hexamerally-arranged exsert septa, a columella composed of two elements, and a much greater calicular diameter.

Occurrence.—Arroyo Zalaya (?Gurabo Formation): loc. TU 1227A.

Distribution.—Miocene: Dominican Republic; Recent: Caribbean, Gulf of Mexico, Bermuda, Madeira, Azores, Persian Gulf, Hawaiian Islands, 28–653 m (Cairns, 1979, 1984).

Suborder **DENDROPHYLLIINA**
Vaughan and Wells, 1943

Family **DENDROPHYLLIIDAE** Gray, 1847

Genus **DENDROPHYLLIA** Blainville, 1830

Diagnosis.—Colonial; dendroid or bushy colonies formed by extratentacular budding; free or attached. Synapticulothecate, with well-developed costae. Septa arranged in Pourtalès Plan (see Wells, 1956, p. F341). Columella spongy; pali often present. Endothecal dissepiments common.

Type-species.—*Madrepora ramea* Linnaeus, 1758, by subsequent designation (Milne-Edwards and Haime, 1850).

Distribution.—Eocene to Recent, cosmopolitan.

Dendrophyllia cornucopia Pourtalès, 1871
Plate 11, figures 14–17

Dendrophyllia cornucopia Pourtalès, 1871, p. 45, pl. 5, figs. 7–8; Cairns, 1979, pp. 179–181, pl. 36, figs. 1–4 (synonymy); Zibrowius, 1980, pp. 175–176, pl. 88, figs. A–L; Hubbard and Wells, 1986, p. 139, figs. 33–35.
Dendrophyllia, n. sp. A of Vaughan and Woodring, 1921, p. 135.
Balanophyllia sp. of Vaughan and Woodring, 1921, p. 135.

Description.—Corallum cylindrical and often slightly curved: up to 55 mm long and 14.2 mm in calicular diameter. Synapticulotheca covered by epitheca, which obscures porosity of corallum. Costae equal in width (about 0.98 mm wide) and flat, separated by shallow grooves about 0.20 mm in width. Costae covered with numerous fine granules, each about 0.10 mm in diameter. No buds or bud scars present on any fossil specimens.

Septa hexamerally arranged in four cycles, sometimes with pairs of S5 in half-systems adjacent to principal septa. Higher cycle septa arranged in a Pourtalès Plan (see Wells, 1956, p. F341). Pali lacking. Columella massive, composed of an elliptical spongy mass of trabeculae. Thin horizontal dissepiments, each traversing one to four interseptal loci, are common.

Diagnostic characters.—Recumbent, subcylindrical corallum; no buds.

Type-material.—MCZ 5442, 2752, syntypes from U. S. Coast Survey Steamer *Bibb* stations 135 and 173, respectively; unnumbered BM(NH) syntype from *Bibb* sta. 173.

Type-locality.—Off Key West, Florida, 220–229 m, Recent.

Material.—Unnumbered NMB specimens from locs. NMB 15806 (3); 15807 (2); 15815 (2); 15836 (2); USNM 64227 (5) from loc. USGS 8528; USNM 64225 (1) from loc. USGS 8545; USNM 64226 (2) from loc. USGS 8733; USNM 63041 (2) from loc. USGS 8735; 2 unnumbered specimens from loc. TU 1210. Reference specimens: specimens listed by Cairns (1979); MCZ 5442, 2752 (syntypes).

Remarks.—The only difference noted between the Recent specimens and the fossils from the Dominican Republic is that the latter lack evidence of buds on all specimens examined. Buds and(or) bud scars are common on almost all Recent specimens.

Vaughan and Woodring's (1921, p. 135) *Dendrophyllia* n. sp. A (USNM 63047 from loc. USGS 8735; USNM 64226 from loc. USGS 8733) and *Balanophyllia* sp. (USNM 63041 from loc. USGS 8735) were examined and identified as *D. cornucopia,* but Vaughan and Woodring's *Dendrophyllia* n. sp. B from loc. USGS 8546 could not be found in the collections of the NMNH.

Comparisons.—*Dendrophyllia cornucopia* is the only species of *Dendrophyllia* thus far reported from the Caribbean Miocene. A species of a related genus, *Balanophyllia pittieri* Vaughan, 1919, is known from the Miocene of Costa Rica. There are two other Recent species of *Dendrophyllia* from the Caribbean: *D. gaditana* (Duncan, 1873) and *D. alternata* Pourtalès, 1880. They are easily distinguished by their branching patterns (Cairns, 1979).

Occurrence.—Río Gurabo (Gurabo and Mao formations) late Miocene to early Pliocene (Text-fig. 3): locs. NMB 15806, 15807, 15815, 15836, locs. USGS 8545, 8735, loc. TU 1210. Río Mao (?Gurabo Formation) late Miocene: locs. USGS 8528, 8733.

Distribution.—Late Miocene to early Pliocene: Dominican Republic; Recent: Atlantic Ocean, 132–960 m (Cairns, 1979).

NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC

6. The Phylum Brachiopoda

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ABSTRACT

Four species of articulate brachiopods: *Tichosina*? *lecta* (Guppy, 1866); *Terebratulina cailleti* Crosse, 1865; *Argyrotheca johnsoni* Cooper, 1934; and *Lacazella caribbeanensis* Cooper, 1977 have been described and illustrated from the Río Gurabo, Río Cana and Arroyo Zalaya sections of the Neogene of the Dominican Republic. *T.*? *lecta* and *L. caribbeanensis* have previously been recorded from the Tertiary of the Caribbean area; *A. johnsoni, T. cailleti* and *L. caribbeanensis* from the Recent of the same region.

Brachiopod occurrences in the Dominican Republic Neogene generally support the paleoecological reconstruction of Saunders, Jung, and Biju-Duval (1986) of increasingly deeper-water conditions proceeding upsection and downstream in both the Río Gurabo and Río Cana valleys.

RESUMEN

Cuatro especies de braquiópodos articulados: *Tichosina*? *lecta* (Guppy, 1866); *Terebratulina cailleti* Crosse, 1865; *Argyrotheca johnsoni* Cooper, 1934; y *Lacazella caribbeanensis* Cooper, 1977 han sido descritos e illustrados de los secciones del Río Gurabo, Río Cana y Arroyo Zalaya del Neógeno de la República Dominicana. *T.*? *lecta* y *L. caribbeanensis* han sido identificados previamente del Terciario del área del Caribe; *A. johnsoni, T. cailleti* y *L. caribbeanensis* del Reciente de la misma región.

El hallazgo de braquiópodos en el Neógeno de la República Dominicana por lo general soporta las reconstrucciones paleoecológicas de Saunders, Jung, y Biju-Duval (1986) de condiciones de aguas más profundas procediendo sección arriba y río abajo en los valles de los ríos Gurabo y Cana.

INTRODUCTION

Tertiary brachiopods are relatively rare in the Caribbean region compared to the comparative abundance and diversity of this group in modern seas in the West Indies (Cooper, 1979). The collections from the Neogene of the Dominican Republic reflect this paucity of fossil taxa, resulting from normal taphonomic information loss, as well as a general reduction in articulate brachiopod diversity following the episode of mass extinction at the end of the Cretaceous.

Specimens collected by the Natural History Museum, Basel [NMB] expeditions to the Dominican Republic between 1978 and 1980 came mainly from the Río Gurabo section (locs. NMB 15823, 15827 [=16084], 15828 [=16095], 15829 [=16104], 15838, 15840, 15851, 15853, 15942 [=15807], and 16811), with small collections from the Río Cana section (locs. NMB 16884 and 17023). In addition Tulane University material was available from the Río Gurabo section (locs. TU 1210, 1211, 1215, and 1300) and the Arroyo Zalaya section (loc. TU 1227A). The location of these sections is shown in Text-figure 1 and the approximate positions of the brachiopod-bearing horizons in the stratigraphic sections from these three river valleys are shown in Table 1. More detailed maps and columnar sections of these valleys, with locality numbers, may be found in Saunders, Jung, and Biju-Duval (1986, text-figs. 4–6, 15, 16, and 36), while a detailed register of both NMB and TU macrofossil collecting localities is shown in appendices 3 and 4 of the same publication.

Systematic paleontological studies of Caribbean Tertiary brachiopods have been made mainly by Cooper (1955, 1959, 1979), while Recent brachiopods from the same region have been described by several authors, most notably Cooper (1977), in which reference to earlier studies is made. Since many Tertiary forms are extant today, such studies are of particular relevance to Tertiary brachiopod paleontology. The standard for Cenozoic brachiopod systematics has been set by G. A. Cooper of the National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. and the present work has relied extensively on his publications on Tertiary (Cooper, 1979) and Recent (Cooper, 1977) brachiopods.

ERRATA

*The measured and(or) figured hypotypes from the Dominican Republic that appear in "Neogene Paleontology in the northern Dominican Republic. 6. The Phylum Brachiopoda", by Alan Logan (***Bulletins of American Paleontology***, volume 93, Number 328, pp. 44-52, plate 12), are the property of the Naturhistorisches Museum Basel and are deposited in that institution.*

By error, catalogue numbers of the United States National Museum of Natural History (USNM) have been assigned to them. The following list shows the correlation of USNM and NMB catalogue numbers:

Tichosina *?* ***lecta*** *Guppy*
USNM 410560 = NMB L 9587
USNM 410561 = NMB L 9588
USNM 410562 = NMB L 9589
USNM 410563 = NMB L 9590
USNM 410564 = NMB L 9591

Terebratulina cailleti *Crosse*
USNM 410565 = NMB L 9592
USNM 410566 = NMB L 9593
USNM 410567 = NMB L 9594
USNM 410568 = NMB L 9595
USNM 410569 = NMB L 9596

Argyrotheca johnsoni *Cooper*
USNM 410572 = NMB L 9597
USNM 410573 = NMB L 9598
USNM 410574 = NMB L 9599
USNM 410575 = NMB L 9600
USNM 410576 = NMB L 9601
USNM 410577 = NMB L 9602
USNM 410578 = NMB L 9603
USNM 410579 = NMB L 9604
USNM 410580 = NMB L 9605

Lacazella caribbeanensis *Cooper*
USNM 410583 = NMB L 9606
USNM 410584 = NMB L 9607
USNM 410585 = NMB L 9608

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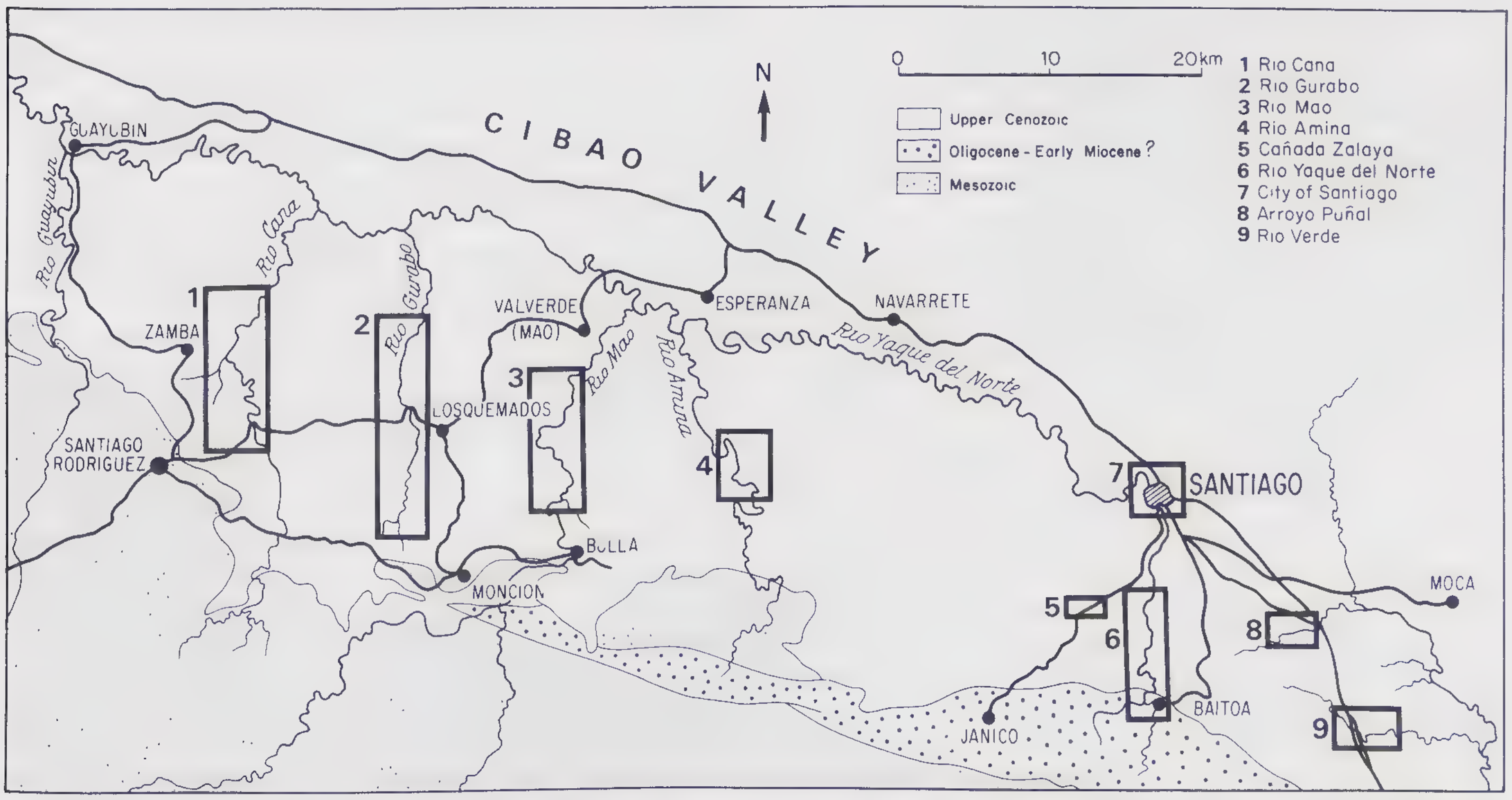
PALEOECOLOGY

Present-day articulate brachiopods are always marine and benthic and there is no reason to suppose that fossil species, particularly in the Tertiary, were otherwise. The presence of pediculate and cementing forms usually implies the initial availability of some kind of hard substrate, either rock or pebbles, for attachment. However, studies made to date suggest that modern forms are generally not sensitive indicators of other environmental variables, such as depth, salinity and water clarity. Species of *Pelagodiscus* Dall, 1908, and *Abyssothyris* Thomson, 1927, for example, seem to be restricted to waters deeper than 500 m, while most other brachiopods, particularly diminutive forms, prefer depths between 0 and 500 m (Zezina, 1970) but, as Cooper (1977) points out, the relatively broad depth ranges of modern species make them unreliable bathymetric indicators where the same or related species occur in the fossil record.

The Dominican Republic collections contain species belonging to the genera *Argyrotheca* Dall, 1900, *Lacazella* Munier-Chalmas, 1881, *Terebratulina* d'Orbigny, 1847, and (?) *Tichosina* Cooper, 1977. Of the 10 named species of *Argyrotheca* recognized by Cooper (1977) from modern seas in the Caribbean area, nine are restricted to the depth range 0–500 m (with four less than 100 m) and the tenth, *A. barrettiana* (Davidson, 1866), is usually found in waters less than 200 m in depth, although occasional specimens may range down to 1473 m (Cooper, 1977). Similarly, all three species of *Argyrotheca* from the Mediterranean Sea



Text-figure 1.—Geological sketch map of the Cibao Valley, showing the location of the Río Cana, Río Gurabo, and Arroyo Zalaya sections from which brachiopods have been collected. (More detailed maps of these sections, with locality numbers, appear in Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 4–5, and 36, respectively.)

prefer depths of less than 100 m (Logan, 1979). The presence of this genus in untransported sediments thus usually indicates relatively shallow water. Similarly, species of the cementing form *Lacazella* usually occur in shallow waters in modern seas. *Lacazella caribbeanensis* Cooper, 1977, has so far been found in less than 100 m depth in the Caribbean (Cooper, 1977), while the closely-related *L. mediterranea* (Risso, 1826) from the Mediterranean and eastern Atlantic (Logan, 1979, 1983), although ranging down to 600 m, is commonest

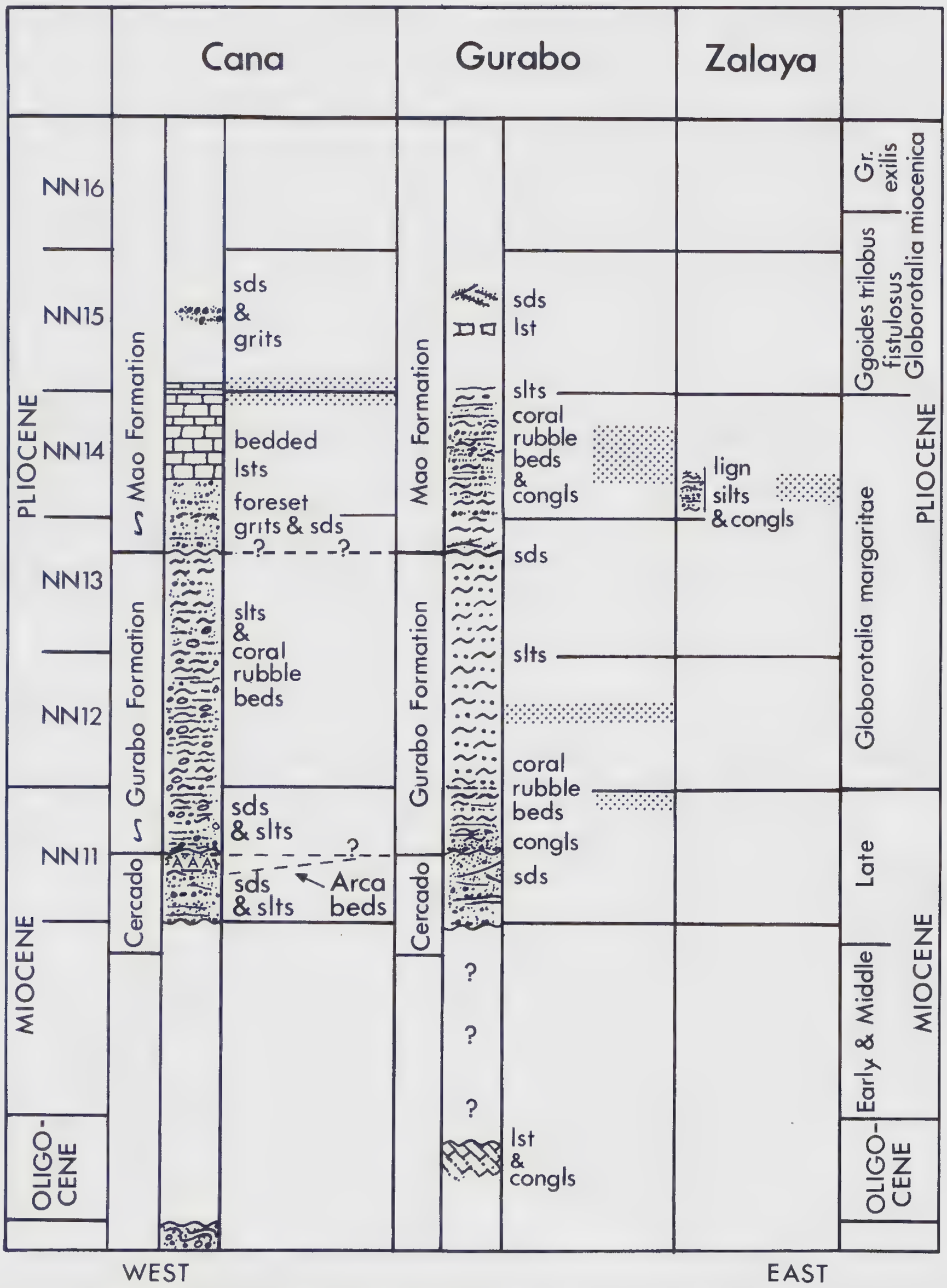


Table 1.—Stratigraphic sections from Río Cana, Río Gurabo, and Arroyo Zalaya, showing approximate positions of brachiopod-bearing horizons (stippled). Approximate stratigraphic correlations after Saunders, Jung, and Biju-Duval (1986). More detailed columnar sections appear in their text-figures 4, 6 (Río Gurabo); and 15, 16 (Río Cana).

in depths of less than 200 m. The commonest living species of *Terebratulina* [*T. retusa* (Linnaeus, 1758) from the eastern Atlantic and Mediterranean, *T. septentrionalis* (Couthouy, 1838) from the western Atlantic and *T. cailleti* Crosse, 1865 from the Caribbean] all range down below 500 m (Cooper, 1977; Logan, 1979, 1983), although *T. septentrionalis* occurs in great abundance above 50 m in the Bay of Fundy (Noble, Logan, and Webb, 1976), and all species are commonest at depths below 300 m. Species of *Tichosina* range down to 1000 m in the Caribbean and are rarely found in depths of less than 100 m (Cooper, 1977), suggesting deeper-water conditions where found *in situ.*

The paleoecological reconstructions proposed by Saunders, Jung, and Biju-Duval (1986) for Neogene strata in the Dominican Republic can now be examined in the light of the above observations on the depth preferences of modern brachiopods, bearing in mind that most of the fossil brachiopods show little evidence of extensive wear-and-tear or disarticulation normally associated with transported assemblages. The base of the Gurabo Formation is about 150 m above the base of the Río Gurabo section and calcareous silts between 250 and 400 m above the base of the section have yielded *Argyrotheca johnsoni* Cooper, 1934 and *Lacazella caribbeanensis* Cooper, 1977, indicating relatively shallow water conditions. This is compatible with the paleoecological evidence from associated fossils, such as foraminifera and slumped blocks of sediment-enclosed reef corals belonging to *Goniopora* Blainville, 1830, and *Montastraea* Blainville, 1830. These occurrences, presumably derived from nearby reefs, suggest depths greater than 40 m and open ocean circulation, according to Saunders, Jung, and Biju-Duval (1986). Cryptic habitats within the corals may have acted as living sites for these brachiopods, as in modern environments (Jackson, Goreau, and Hartman, 1971; Meile and Pajaud, 1971; Logan, 1977, 1981), where sclerosponges are usually an important part of this community. Mousa (1974) has found a similar association of *Argyrotheca, Lacazella* and reef-associated foraminifera in Oligocene–Miocene claystones from Puerto Rico, which have also yielded sclerosponge-like spicules in wash residues. Such spicules should be sought in the sediment samples from the Dominican Republic as further evidence of derivation from nearby reefs.

The upper part of the Río Gurabo section comprises the Mao Formation, which has yielded *Argyrotheca johnsoni* Cooper, 1934, and *Tichosina*? *lecta* (Guppy, 1866). Saunders, Jung, and Biju-Duval (1986) refer to this part of the section as follows (pp. 16–17): "From about 650 to 750 m on the column a *Limopsis*-Pteropoda mollusc assemblage predominates. This assemblage also includes *Propeamussium,* terebratulid brachiopods, and small solitary corals, and thus points to considerable water depths." The terebratulids referred to are undoubtedly those here questionably assigned to *Tichosina,* a form previously acknowledged to be indicative of deeper-water conditions. Furthermore, both *Tichosina*? *lecta* and *Terebratulina cailleti* Crosse, 1865 are found in association with *Argyrotheca johnsoni* in alternating calcareous siltstones and coral limestones at a slightly higher level in the Mao Formation from the Río Cana section (Table 1). Mainly on the basis of foraminifera, Saunders, Jung, and Biju-Duval (1986) suggest water depths of at least 100 m. The brachiopod evidence of *T.*? *lecta* and *T. cailleti* is not inconsistent with this reconstruction, although the deepest recorded occurrence of *A. johnsoni* from the present day is 72 m (Logan, 1977).

Thus in both the Río Gurabo and Río Cana sections the sedimentary and fossil evidence indicates increasingly deeper water conditions due to increasing distance from the paleo-shoreline as one proceeds downriver and upsection, notwithstanding the different lithologies in the two sections. The Arroya Zalaya section has only a single brachiopod-bearing locality, which has yielded *Argyrotheca johnsoni* Cooper, 1934, indicative at present of water of less than 72 m depth (Logan, 1977). The associated foraminifera and other evidence suggest open marine conditions, moderate water depths and relatively low water-energy levels, according to Saunders, Jung, and Biju-Duval (1986).

BIOSTRATIGRAPHY

Brachiopods are generally intolerant of a wide variety of substrate types and, since they evolve slowly, are generally regarded as of limited value in biostratigraphy. *Lacazella caribbeanensis* Cooper, 1977 ranges from the Miocene to the present, while *Tichosina*? *lecta* (Guppy, 1866) is recorded from the Eocene of Cuba by Cooper (1979). Both *Argyrotheca johnsoni* Cooper, 1934, and *Terebratulina cailleti* Crosse, 1865, are common in modern seas off the West Indies but have not previously been recorded from the Tertiary.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Taxonomic studies on both Recent and fossil brachiopods have traditionally been carried on mainly by paleontologists, since this phylum was much more diverse in the past than it is at the present time. This has resulted in a consistent approach to the classification of the group as a whole and the description of taxa at various levels, with emphasis on shell characteristics rather than soft parts, as one might expect in a predominantly fossil group. The classification of Williams and Rowell (1965) has been adopted here; this volume of the *Treatise* also contains detailed de-

scriptions of all supra-specific categories and a glossary of terms, an abbreviated version of which can be found in Logan (1979).

PHILOSOPHICAL CONSIDERATIONS

Cooper (1970, 1977) has outlined the main characters used in the recognition of species and genera of brachiopods, noting the emphasis on external shell features at these lower levels, in contrast to the importance of internal shell characters at family and higher taxonomic levels. The ornament and shell shape, together with the nature of the brachial skeleton, are the main generic characters used, with size, ornament, shell shape and shell coloration (mainly with Recent species) as the most important specific characters. The density of punctae varies greatly with the size of the individual and the position of the area sampled on the shell; consequently it has not proved to be a reliable specific characteristic, except in certain cases (Foster, 1974).

While there is general agreement among brachiopod taxonomists on the nature of the characters to be used for distinguishing taxa, there is less conformity of opinion on how narrowly brachiopod genera should be defined or on what is the limit of permissible variation within a species. Those taxonomists conversant with Recent species are well aware of the variation in size and shape associated with ontogeny and usually append scatter diagrams to species descriptions (*e.g.,* Logan, 1979). This is less easy to do with fossil species, where the number of actual specimens from a locality may be small and in these cases differences in practice arise among paleontologists. My own philosophy is to take the broad view of a species, based on natural variation, and to avoid the proliferation, whenever possible, of large numbers of species based on small samples.

FORMAT, MEASUREMENTS, AND ACRONYMS OF SPECIMEN REPOSITORIES

Citations included in the synonymy of each species are those considered to have identity with the described species. Measurements of figured specimens are in millimeters and include the length of each valve, maximum width and thickness, where able to be measured; these and other dimensions can also be obtained from the figures. All figured specimens have been deposited in the U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (formerly the United States National Museum) and bear USNM repository numbers. All other specimens examined have been returned to the Natural History Museum, Basel, Switzerland [NMB], including some Tulane University [TU] material given to the author by Dr. Emily Vokes.

Class **ARTICULATA** Huxley, 1869

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATULIDINA** Waagen, 1883

Superfamily **TEREBRATULACEA** Gray, 1840

Family **TEREBRATULIDAE** Gray, 1840

Subfamily **TEREBRATULINAE** Gray, 1840

Genus **TICHOSINA** Cooper, 1977

Type-species.—*Tichosina floridensis* Cooper, 1977, Recent, West Indies.

Tichosina? lecta (Guppy)
Plate 12, figures 1–13

Terebratula lecta Guppy, 1866, p. 296, pl. 19, fig. 3.
Tichosina? lecta (Guppy). Cooper, 1979, p. 11, pl. 2, figs. 1–5.

Diagnosis.—Anteriorly-tapering *Tichosina*? with a narrow anterior fold.

Type material.—Cooper (1979) states that this species is based on three specimens, all of them poorly preserved. The lectotype (USNM 115646a) is measured and figured (his pl. 2, figs. 1–5, where it is incorrectly referred to as the holotype), while a syntype (USNM 115646b) is also measured.

Horizon and type locality.—Eocene, USNM locality 818o, San Fernando, Trinidad.

Material.—Fragmentary material from localities NMB 15828 (14 fragments) and 15829 (about 30 fragments) from the Río Gurabo section, locality NMB 16884 (nine fragments) from the Río Cana section and locality TU 1300 (three relatively complete specimens and eight fragments) from the Río Gurabo section, the complete specimens showing some post-mortem distortion and fracturing.

Measurements (in mm).—

	pedicle valve length	*brachial valve length*	*maximum width*	*thickness*	*apical angle (degrees)*
USNM 410560	29.7	25.8	23.9	15.0	82
USNM 410561	37.6	31.7	23.9	23.7	71
USNM 410562	31.9	26.4	25.3	16.9	100

Remarks and comparisons.—The relatively poor preservation of the Dominican Republic material and the absence of a complete loop in any of the specimens examined preclude positive identification with the genus *Tichosina,* although one specimen (Pl. 12, fig. 13) shows the flat-bladed crural bases typical of the genus. The external shape, size and labiate permesothyridid foramen also suggest *Tichosina.* The general dimensions are closest to *T.*? *lecta* from the Eocene of Trinidad, the type material of which was recently re-figured by Cooper (1979). While the uniplicate anterior commissure varies in intensity of development of the fold,

post-mortem distortion may account for some of these differences. Thus one example from the Dominican Republic (USNM 410561) is narrower and more globose than typical *T.? lecta* and has a more developed uniplicate anterior margin, resembling that of *T.? bartletti* (Dall, 1920) from the Recent of Barbados (Cooper, 1977, 1979). None of the other Recent species of *Tichosina* described by Cooper (1977) is closely comparable with *T.? lecta*; most are more globose and have a more exaggerated uniplicate anterior margin.

Occurrence and distribution.—The occurrence of this species in the Dominican Republic has already been documented (see *Material* above). The type material is from the Eocene of Trinidad and the species has not previously been recorded from any other area.

Family **CANCELLOTHYRIDIDAE** Thomson, 1926

Subfamily **CANCELLOTHYRIDINAE** Thomson, 1926

Genus **TEREBRATULINA** d'Orbigny, 1847

Type-species.—*Anomia retusa* Linnaeus, 1758, Recent, off Norway.

Terebratulina cailleti Crosse
Plate 12, figures 14–22

Terebratulina cailleti Crosse, 1865, p. 27, pl. 1, figs. 1–3.
Terebratulina cailleti Crosse. Davidson, 1886, p. 26, pl. 5, figs. 41–42.
Terebratulina cailleti Crosse. Cooper, 1977, p. 99, pl. 25, figs. 1–16; pl. 28, figs. 4–27.

Description.—Shell small, rarely exceeding 10 mm in length in adult forms, ovate to sub-pentagonal, longer than wide, slightly auriculate at hinge line, particularly in juvenile stages, apical angle of pedicle valve less than 90°; biconvex, brown in living specimens, punctate, costellate, with eight to 10 primary costellae, secondary costellae intercalated anteriorly. Costellae strongly beaded, particularly in juveniles. Anterior commissure uniplicate, with shallow ventral sulcus and dorsal fold. Foramen large, mesothyridid, with pedicle collar; deltidial plates disjunct.

Brachial skeleton extends to almost half length of brachial valve; hinge plates absent, socket ridges and crural bases fused to form prominent ridges. Crura convergent, crural processes uniting to form a ring-like loop with ventrally-arched transverse ribbon.

Cardinal process small, transverse; hinge teeth grooved on inner face. Small oval-shaped muscle impressions in both valves, interiors of both valves with branching mantle canals; lophophore plectolophous, spicules abundant.

Diagnosis.—Small elongate-oval *Terebratulina* with beaded costellae.

Type material.—The whereabouts of Crosse's type material is unknown.

Horizon and type locality.—Recent, Guadeloupe, West Indies.

Material.—A complete brachial valve from locality NMB 16884 and a complete bivalved specimen and three separate pedicle valves from locality NMB 17023, all juveniles and from the Río Cana section.

*Measurements.**—

	pedicle valve length	*brachial valve length*	*maximum width*	*thickness*	*apical angle (degrees)*
USNM 410565	—	5.1	4.1	—	105
USNM 410566	5.4	—	4.0	—	72
USNM 410567	5.0	4.5	3.8	2.0	74
USNM 410568	—	3.0	2.3	—	60
USNM 410569	—	2.9	2.0	—	61
USNM 410570	6.6	6.0	4.7	2.1	55 (97)
USNM 410571	7.0	6.2	6.0	2.6	71 (93)

Remarks and comparisons.—Although none of the Dominican Republic specimens show the diagnostic loop, the external features of both valves and the internal features of the pedicle valve are typical of the genus *Terebratulina* rather than *Eucalathis* Fischer and Oehlert, 1890, or *Chlidonophora* Dall, 1903. The fossil material is identified with the Recent species *T. cailleti* Crosse, which is common in the waters around the West Indies. This species was recently extensively reillustrated by Cooper (1977) and specimens dredged from 125 to 150 m depth off Paynes Bay, Barbados have been figured here for comparison with the fossil forms. All the fossil specimens appear to be juveniles but show the typical elongate-oval shape and beaded costellae typical of the species. As Cooper (1977) has remarked, *T. cailleti* is generally smaller than its more northern congeners, *T. septentrionalis* (Couthouy, 1838), and *T. retusa* (Linnaeus, 1758), the largest specimen of *T. cailleti* in the collection from Barbados measuring 13.0 mm in pedicle valve length and 11.2 mm in maximum width. *Terebratulina retusa* was recently re-described by Logan (1979) and compared in detail to *T. septentrionalis*. *T. cailleti* differs from both these species and from *T. latifrons* Dall, 1920 in being much smaller when fully grown, more elongate and with strongly-beaded costellae (Cooper, 1977). In addition, *T. latifrons* is sub-triangular in outline, with a stronger fold and sulcus, and is similar in these respects to the Miocene species *T.? palmeri* described by Cooper (1979) from Cuba.

Occurrence and distribution.—The occurrence of this species in the Neogene of the Dominican Republic is

* The number in parentheses under *apical angle* is that of the brachial valve: the other number in such pairs is that of the pedicle valve.

limited to the Río Cana section. The species is previously known only from the Recent, where it is common in the Caribbean region.

Suborder **TEREBRATELLIDINA** Muir-Wood, 1955

Superfamily **TEREBRATELLACEA** King, 1850

Family **MEGATHYRIDIDAE** Dall, 1870

Genus **ARGYROTHECA** Dall, 1900

Type-species.—*Terebratula cuneata* Risso, 1826, Recent, Mediterranean.

Argyrotheca johnsoni Cooper
Plate 12, figures 23–41

Argyrotheca johnsoni Cooper, 1934, p. 2, pl. 1, fig. 10, pl. 2, figs. 1–12.
Argyrotheca johnsoni Cooper. Cooper, 1977, p. 111, pl. 1, figs. 2–7.

Description.—Adult shell wider than long, rarely exceeding 8 mm in width at its widest point, variable in outline from alate to semicircular, cardinal extremities occasionally mucronate; biconvex to almost planoconvex, pedicle valve more convex than brachial valve; anterior commissure shallowly sulcate; ventral interarea broadly triangular, flat, catacline to weakly apsacline, dorsal interarea very narrow, anacline. Beak short, subtruncate, usually abraded, foramen large, hypothyridid, with pedicle collar, delthyrium flanked by rudimentary narrow deltidial plates. Ornament of low, gently-rounded costae, usually four to seven in number, with occasional costae intercalated in sulcus–fold region, interspaces narrow, cream to pale yellow in living forms, in contrast to pink tinges at extremities of ribs. Shell coarsely punctate.

Interior of pedicle valve shows widely-separated teeth along denticulated hinge area, pedicle collar supported by median septum extending to between about half and four-fifths length of valve, triangular in profile, low and thin. Brachial valve with short, transversely-elongated cardinal process; hinge line with elongate sockets; long median septum reaching almost to anterior margin, apex at mid-valve, triangular in profile, occasionally with four to five serrations sloping steeply to anterior margin. Crura widely separated, crural processes pointed, horizontal; brachial skeleton comprising two arcuate lamellae attached to base of crura, valve floor and slightly posterior of anterior extremity of median septum; muscle scars distinct, lophophore schizolophous.

Diagnosis.—Alate to semicircular *Argyrotheca* with catacline ventral interarea and subdued costae.

Type material.—Holotype: USNM 431003. Paratypes: USNM 431003a–c (Cooper, 1934, 1977).

Horizon and type locality.—Recent, Johnson–Smithsonian Deep Sea Expedition Station 52, Latitude 19°10′25″N, Longitude 69°20′55″W to Latitude 19°10′05″N, Longitude 69°21′25″W, attached to worm tubes in association with *Thecidellina barretti* (Davidson, 1864) at 25–40 m depth off Cape Samaná, Dominican Republic (Cooper, 1934).

Material.—Four complete specimens from locality NMB 15823, one complete specimen from locality NMB 15827, two brachial valves from locality NMB 15828, nine pedicle and eight brachial valves from locality NMB 15829, 14 complete specimens and some fragments from locality NMB 15838, two complete specimens and two pedicle valves from locality NMB 15840, a single incomplete brachial valve from locality NMB 15851, a single complete specimen from locality NMB 15853, a complete specimen and two brachial valves from locality NMB 15942 (=15807), a pedicle valve and two brachial valves from locality NMB 16811; all from the Río Gurabo section. One complete specimen and three fragmentary pedicle valves from locality NMB 16884, and a single complete specimen from locality NMB 17023; Río Cana section. Also a single complete example from locality TU 1215 (Río Gurabo section), and three separate pedicle valves from locality TU 1227A (Arroyo Zalaya section).

Measurements (in mm).—

	pedicle valve length	*brachial valve length*	*maximum width*	*thickness*
USNM 410572	2.2	—	3.5	—
USNM 410573	1.9	1.8	3.8	1.9
USNM 410574	1.8	1.8	3.0	1.6
USNM 410575	1.5	1.5	3.0	1.3
USNM 410576	1.5	1.5	2.2	1.3
USNM 410577	3.2	3.0	5.6	1.3
USNM 410578	2.5	2.5	3.8	1.1
USNM 410579	1.7	1.6	4.0	1.9
USNM 410580	2.0	2.0	3.5	1.3
USNM 410581	4.0	3.5	8.0	2.8
USNM 410582	4.8	4.1	7.0	2.8

Remarks and comparisons.—Although many Recent and fossil specimens of *Argyrotheca* have been described from the Caribbean region, very few are strongly alate and have a catacline ventral interarea. The Dominican Republic material is here identified with the modern species *A. johnsoni* Cooper, 1934, notwithstanding the smaller size of the fossil specimens, which are assumed to be immature. Many of the modern species of *Argyrotheca* are distinguished on the basis of shell coloration, clearly inappropriate for the fossil forms, which have lost any coloration they might once have possessed. Two specimens of modern *A. johnsoni* from the type locality are figured (Pl. 12, figs. 36–41) to show the range of variation in shape and number of costae, and for comparison with the figured fossil specimens. Of the other extant species

of *Argyrotheca,* only *A. rubrocostata* Cooper, 1977, *A. schrammi* (Crosse and Fischer, 1866), and *A. rubrotincta* (Dall, 1871) show similarities in outline of shell to *A. johnsoni.* The ribbing in *A. rubrocostata* is generally finer and the ventral sulcus narrower than in *A. johnsoni,* while *A. schrammi* has fewer but more exaggerated ribs, giving a strongly-scalloped anterior margin. This species, as Cooper (1977) has indicated, is poorly known. *A. rubrotincta* has perhaps the strongest resemblance to the fossil forms from the Dominican Republic, but lacks the strongly-alate outline characteristic of this species. None of the Tertiary species described by Cooper (1979) from Cuba and the Caribbean is similar to the species described here.

Occurrence and distribution.—This species occurs in the Neogene of the Dominican Republic in the Río Gurabo and Arroyo Zalaya sections but is otherwise unknown from the fossil record, although relatively common in modern seas in the Caribbean, where it has been recorded from the Dominican Republic [Johnson–Smithsonian Station 52, Pillsbury Station P 1153], north-east of Turks Island, Bahamas [Pillsbury Station P 1421] (Cooper, 1977), off Tongue of Ocean, Bahamas (Logan, 1977), and off the north coast of Jamaica (Jackson, Goreau, and Hartman, 1971).

Type material.—Holotype: USNM 549449a. Paratypes: 549448a, 549449b (Cooper, 1977).

Horizon and type locality.—Recent, Johnson–Smithsonian Deep Sea Expedition Station 52, Latitude 19°10′25″N, Longitude 69°20′55″W to Latitude 19°10′05″N, Longitude 69°21′25″W, in association with *Argyrotheca johnsoni* Cooper, 1934 at 25–40 m depth off Cape Samaná, Dominican Republic (Cooper, 1977). This species may be the "*Thecidellina barretti* (Davidson)" referred to in Cooper (1934).

Material.—Only three specimens of this species are present in the collections: two single brachial valves (from loc. NMB 15942 and loc. TU 1211) and a single pedicle valve (from loc. TU 1215), all from the Río Gurabo section.

Measurements (in mm).—

	pedicle valve length	*brachial valve length*	*maximum width*
USNM 410583	—	1.5	2.2
USNM 410584	—	1.8	2.6
USNM 410585	2.0	—	2.1
USNM 410586	2.6	—	2.7
USNM 250982	3.6	2.5	3.4
USNM 250983	3.6	—	3.5
USNM 250984	—	3.0	3.4

Order **THECIDEIDA** Pajaud, 1970

Suborder **THECIDEIDINA** Elliot, 1958

Superfamily **THECIDEACEA** Gray, 1840

Family **THECIDEIDAE** Gray, 1840

Genus **LACAZELLA** Munier-Chalmas, 1881

Type-species.—*Thecidea mediterranea* Risso, 1826, Recent, Mediterranean.

Lacazella caribbeanensis Cooper
Plate 12, figures 42–49

Thecidium mediterraneum (Risso). Davidson, 1864, p. 21, pl. 2, fig. 5.
Thecidium mediterraneum (Risso). Davidson, 1887, p. 158.
Lacazella mediterranea (Risso). Meile and Pajaud, 1971, p. 470, pl. 1, figs. 1–4.
Lacazella caribbeanensis Cooper, 1977, p. 132, pl. 4, figs. 12–19.
Lacazella caribbeanensis Cooper. Logan, 1979, p. 75, pl. 10, figs. 9–14.
Lacazella caribbeanensis Cooper. Cooper, 1979, p. 28, pl. 1, figs. 2–5.

Description.—This species was recently described and illustrated in detail by Cooper (1977), to which the reader is referred.

Diagnosis.—Small *Lacazella* with hemispondylium attached to the valve floor and the ascending apparatus narrow anteriorly and with smooth margins (Cooper, 1977).

Remarks and comparisons.—In spite of the limited material available, there is no doubt of the identity of the Dominican Republic specimens with *Lacazella caribbeanensis* Cooper, 1977. The distinctive internal features of the brachial valve, mainly the ascending and descending apparatus, clearly indicate that the specimens belong to *Lacazella* rather than *Thecidellina,* the only other modern cemented articulate brachiopod genus. There are three known species of *Lacazella*: *L. mediterranea* (Risso, 1826) from the Mediterranean and eastern Atlantic (Logan, 1979, 1983), *L. mauritiana* Dall, 1920 from the Indian Ocean (Cooper, 1973) and *L. caribbeanensis* Cooper, 1977 from the Caribbean region. The main differences between these three species have been discussed by Cooper (1977, 1979) and Logan (1979). *L. caribbeanensis* is distinguished from its congeners by its smaller size, differently-shaped hemispondylium (two separate plates, rather than a bilobed plate), smoother margins to the ascending apparatus and intervening median ridge of the brachial valve, and more subdued internal markings in both valves. Modern Bahamian material belonging to *L. caribbeanensis* (Pl. 12, figs. 46–49) has been figured for comparison with the fossil forms.

Occurrence and distribution.—This species has been recorded from the Miocene of Cuba (Cooper, 1979); this and the present report of its occurrence in the Neogene of the Dominican Republic are the only fossil

examples so far known. The species has been recorded from modern seas around the Bahamas (Meile and Pajaud, 1971; Logan, 1979) and has recently been identified by the present author attached to a stalagmite at the bottom of the blue hole off South Bight, Andros Island, Bahamas, at a depth of 45 m (in Gascoyne *et al.*, 1979). Elsewhere it has been taken off Jamaica (Davidson, 1864, 1887; Jackson, Goreau, and Hartman, 1971) and the Dominican Republic (Cooper, 1977).

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EXPLANATION OF PLATE 1

Page

Calices and transverse thin-sections of modern ***Stephanocoenia intersepta*** (Lamarck) from three different habitats near Discovery Bay, Jamaica (see Foster, 1980, for locality information) 16

All photos, ×10. The columellar style and septa are thickest in the forereef and thinnest in the lagoon population. The inner wall is also especially thin in the lagoon, and the entire theca is more porous. The pali and septal teeth appear best-developed in the sand channel population.

Figure

1. Figured specimen. SUI 51065, forereef sand channel (20 m depth), SEM of calical surface.
2. Figured specimen. SUI 51073, forereef sand channel (20 m depth), transverse thin-section.
3. Figured specimen. SUI 51080, forereef (20 m depth), SEM of calical surface.
4. Figured specimen. SUI 51082, forereef (20 m depth), transverse thin-section.
5. Figured specimen. SUI 51085, lagoon (16 m depth), SEM of calical surface.
6. Figured specimen. SUI 51085, lagoon (16 m depth), transverse thin-section.

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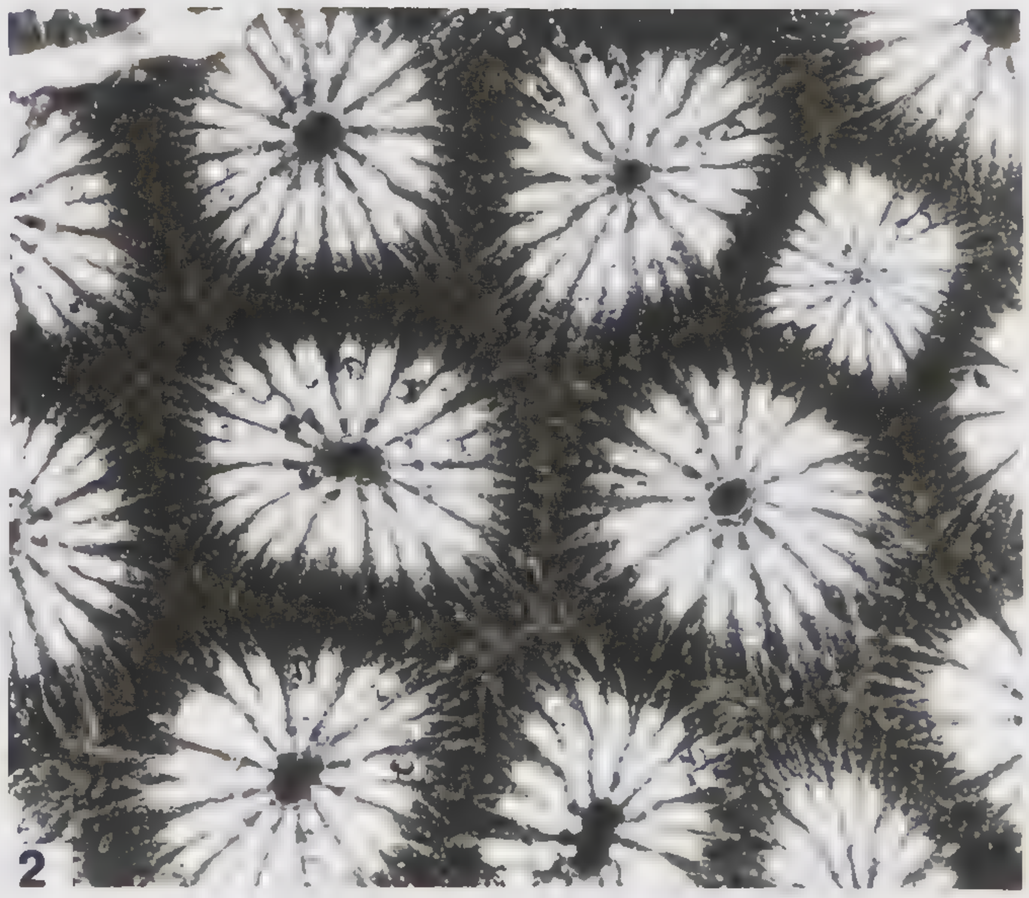
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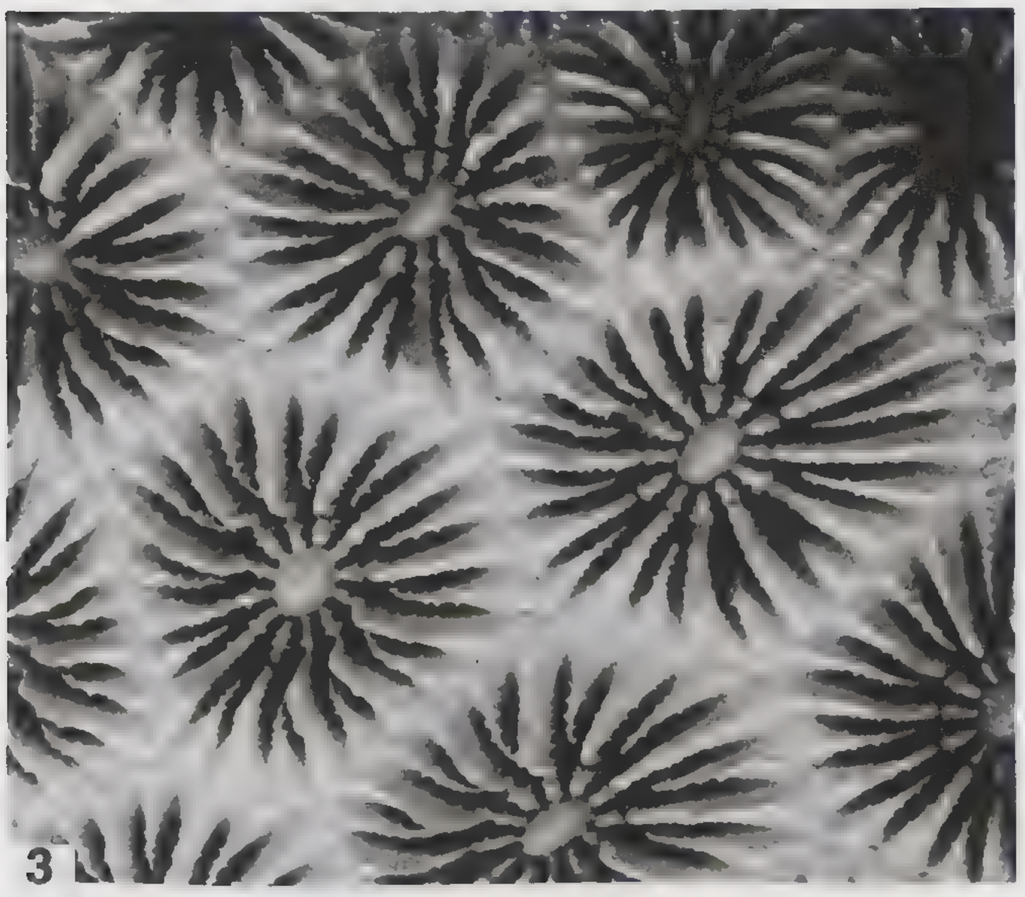
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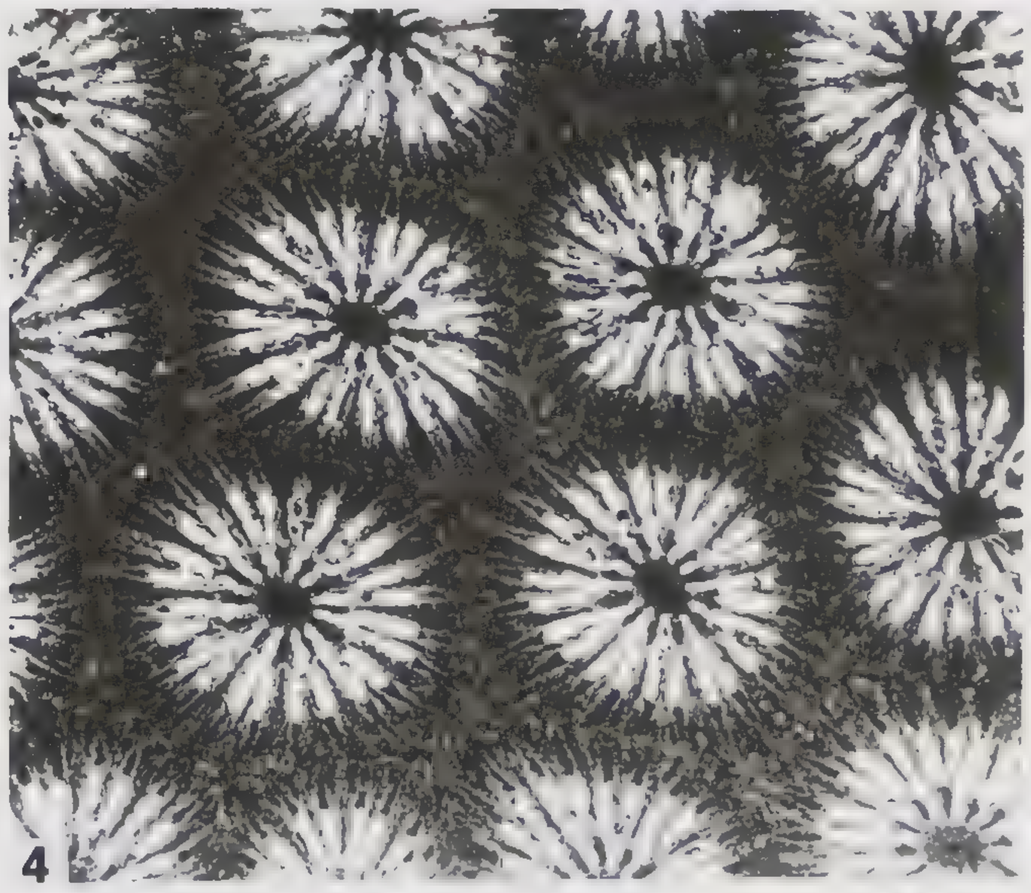
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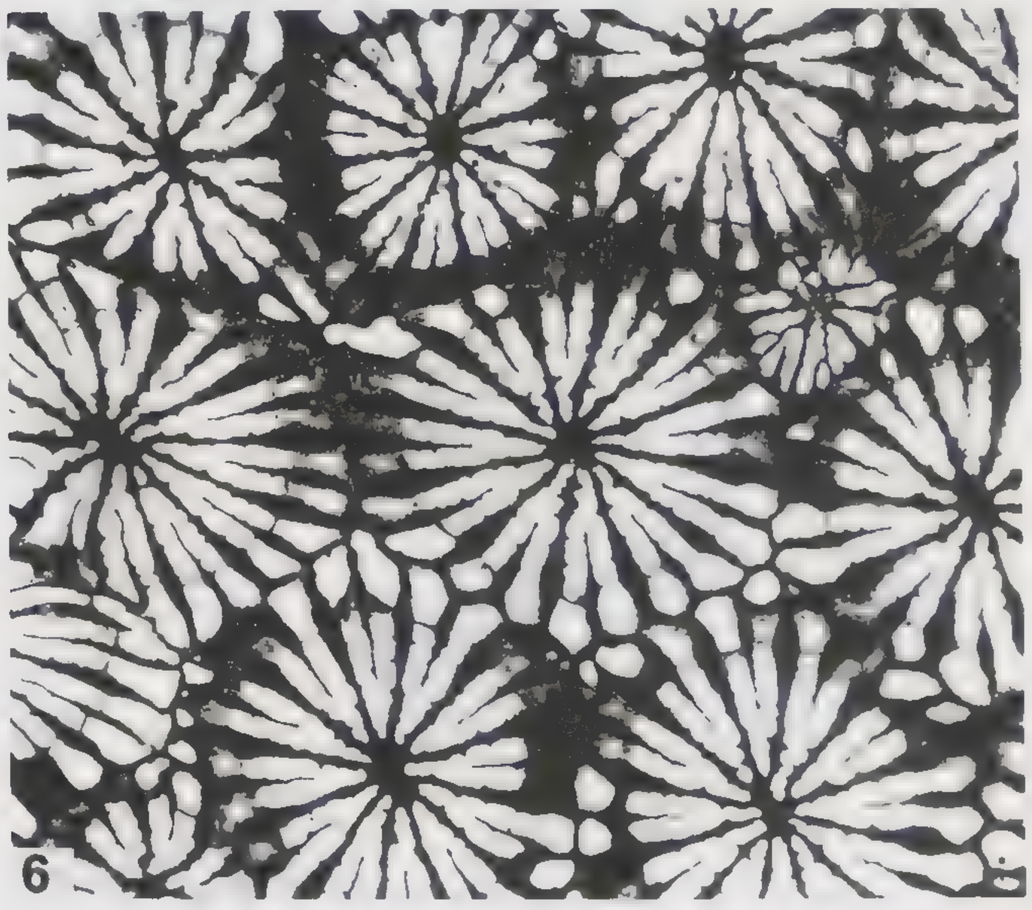
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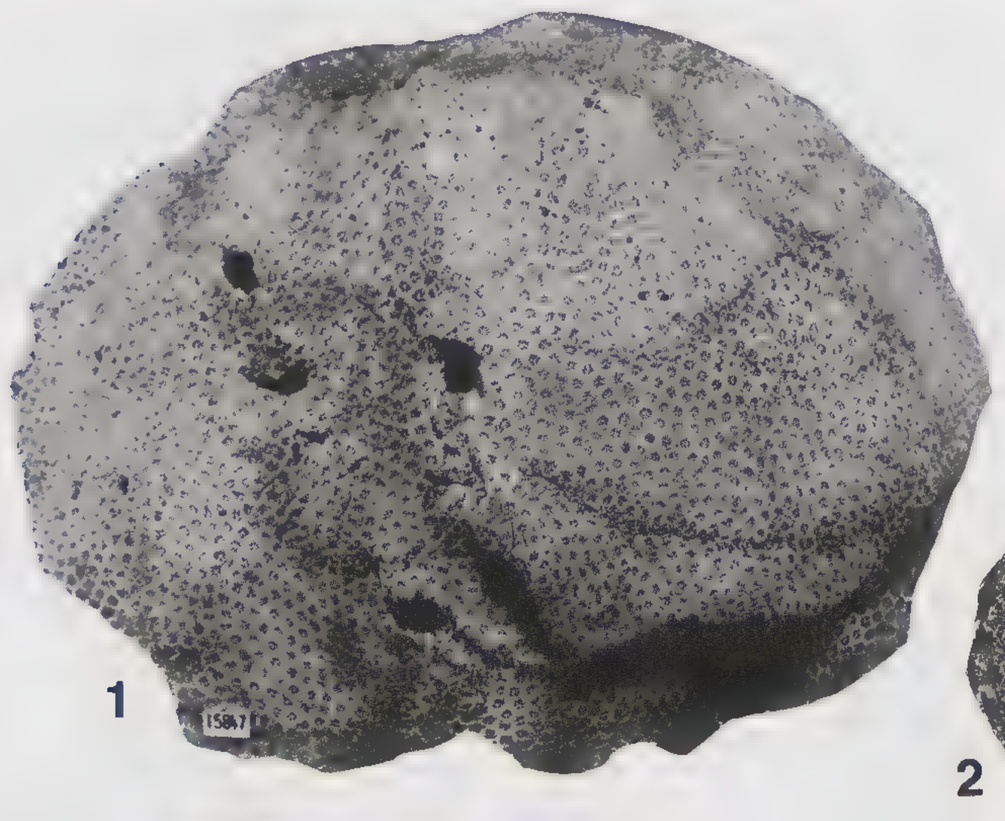

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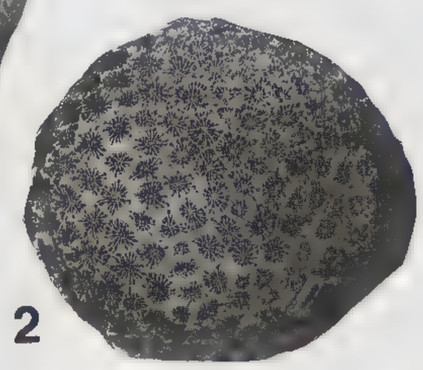

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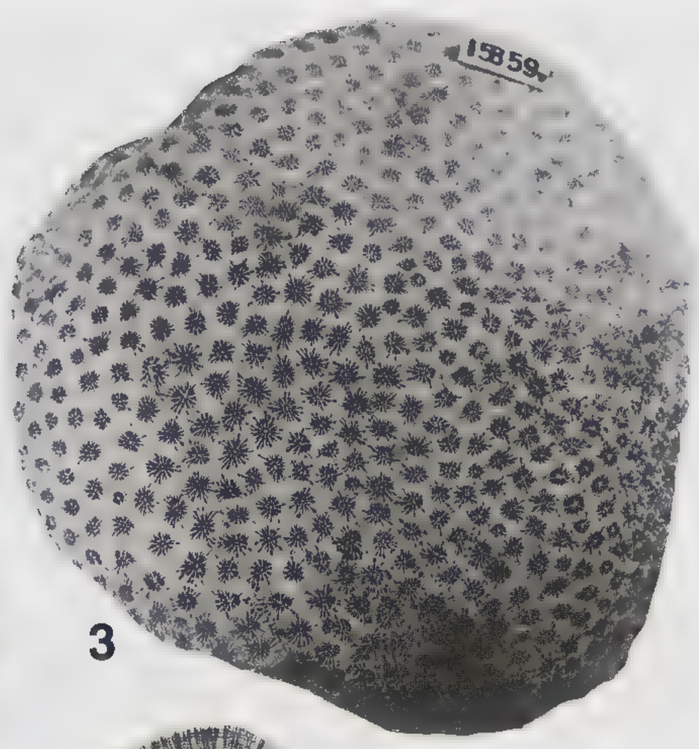

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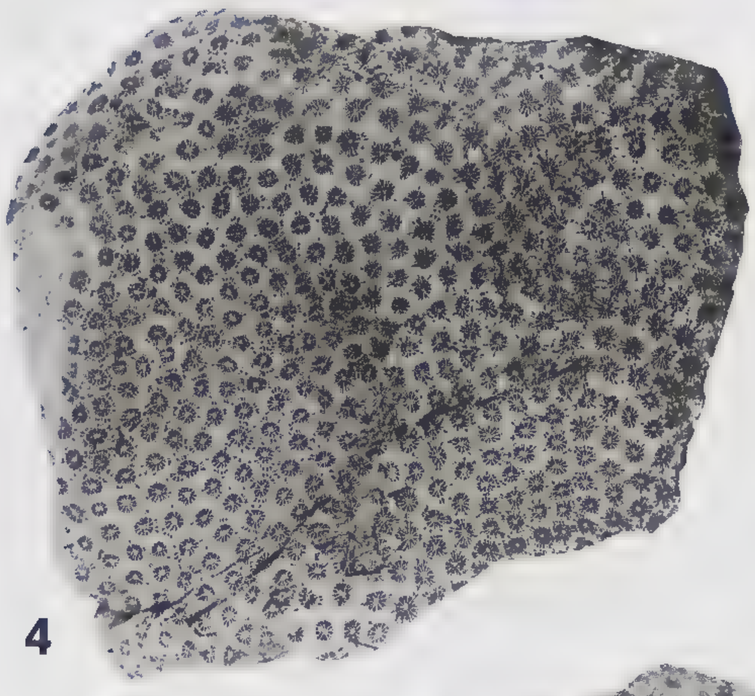

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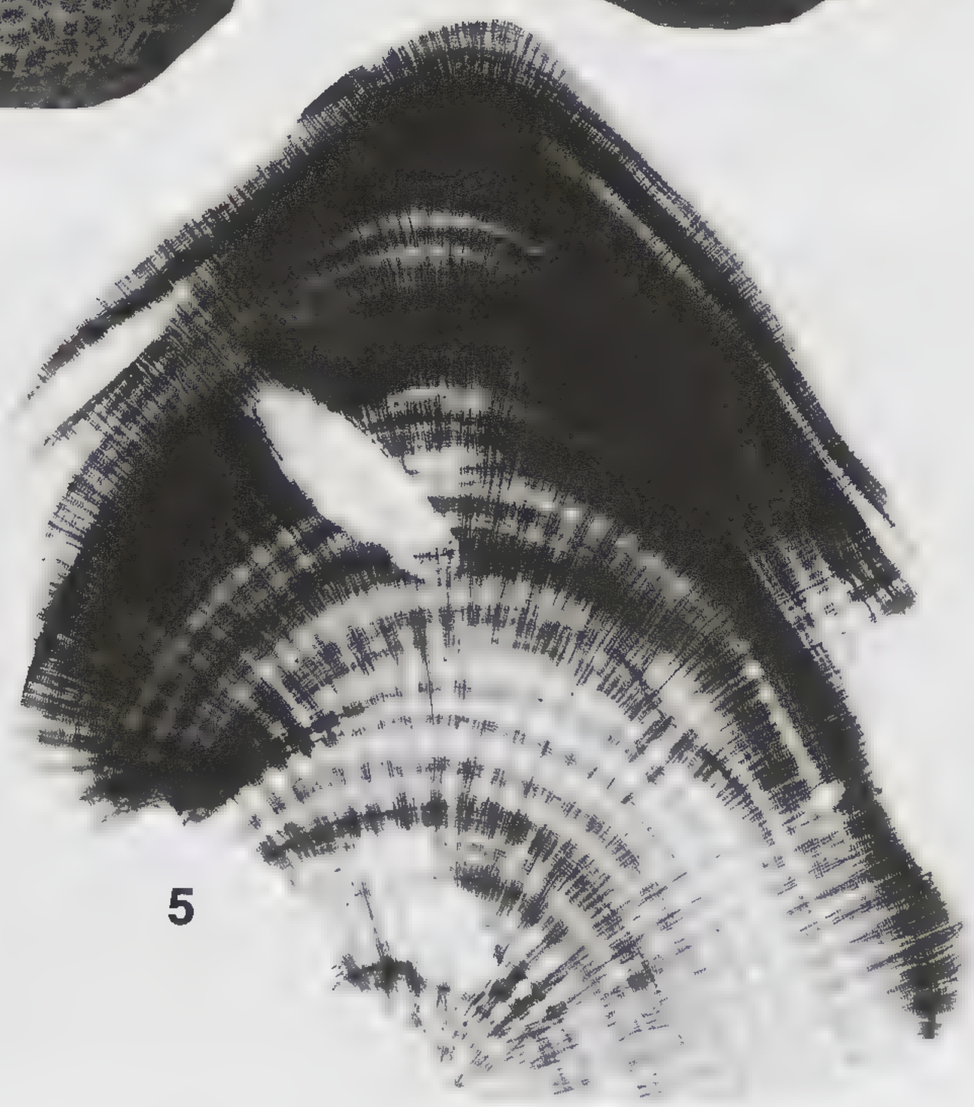

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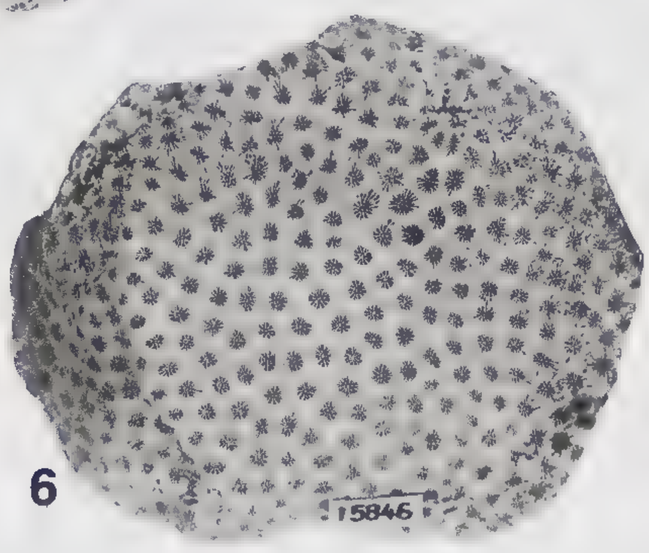

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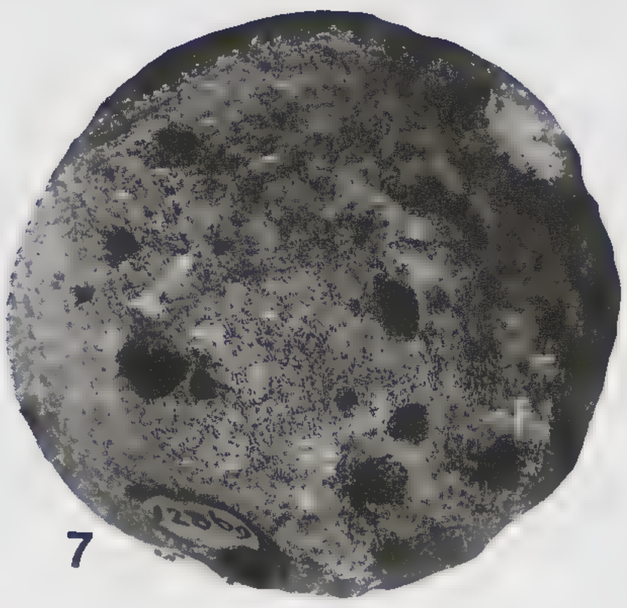

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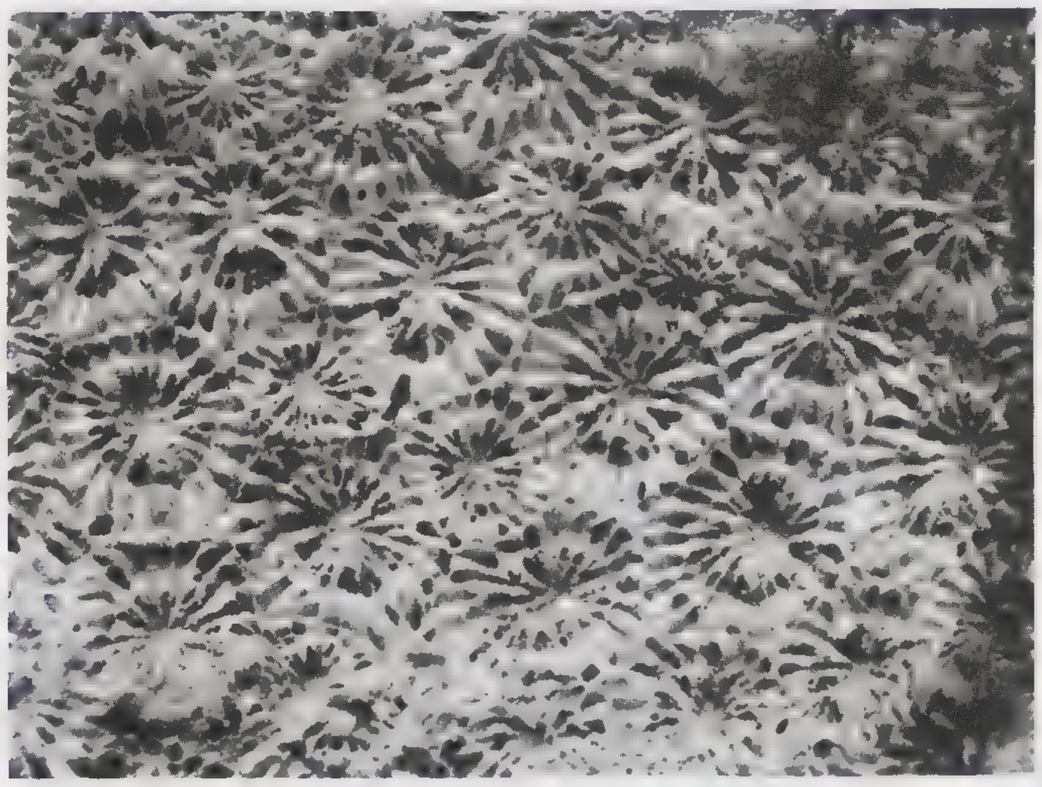

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EXPLANATION OF PLATE 2

Page

Stephanocoenia spongiformis (Duncan) 20

Whole colonies, closeups of calical surfaces, and X-radiographs. Colonies are generally small to intermediate in size and well-rounded with smooth outer surfaces. The calices are small and circular, and the exothecal intercostal area well-developed.

Figure

1. Figured specimen. NMB D5763. Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×½.
2. Figured specimen. NMB D5867. Upper Miocene, locality NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×1.
3. Figured specimen. NMB D5866. Upper Miocene, locality NMB 15859, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×1.
4. Figured specimen. NMB D5793. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×1.
5. Figured specimen. NMB D5762. Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, ×1.
6. Figured specimen. NMB D5792. Upper Miocene, locality NMB 15846. Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×1.
7. Holotype. BM(NH) R28756. Neogene, "silt of the sandstone plain, San Domingo." Upper surface of colony, ×1.
8. Holotype. BM(NH) R28756. Same specimen as figure 7 above. Closeup of calical surface, ×5.

EXPLANATION OF PLATE 3

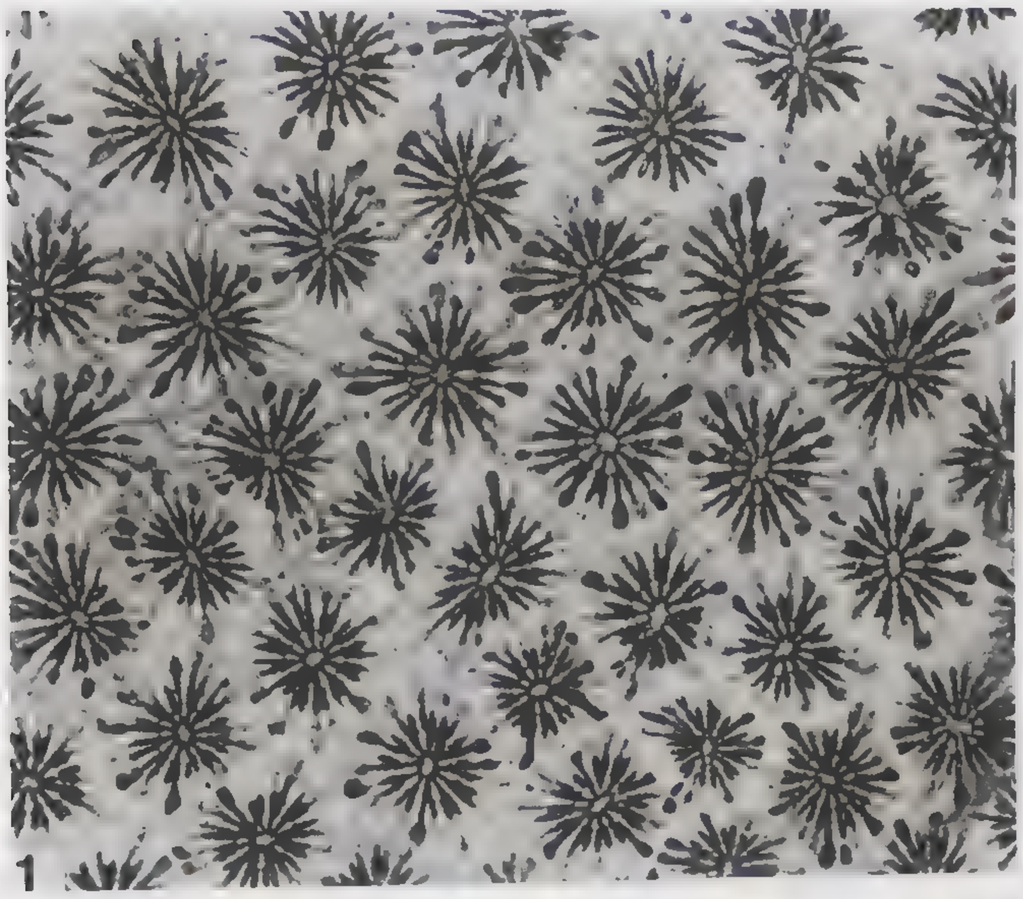
Page

Stephanocoenia spongiformis (Duncan) 20

Closeups of calical surfaces and transverse thin-sections. The exothecal intercostal area has a distinctive appearance with a well-developed second outer wall formed at the junction between calices. The pali are weak and 12 in number. They appear better-developed on the primary septa. The columella forms a prominent style. The tertiary septa are relatively thin and long.

Figure

1. Figured specimen. NMB D5866. Same specimen as Plate 2, figure 3. Calical surface, ×5.
2. Figured specimen. NMB D5761. Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
3. Figured specimen. NMB D5793. Same specimen as Plate 2, figure 4. Calical surface, ×5.
4. Figured specimen. NMB D5762. Same specimen as Plate 2, figure 5. Transverse thin-section, ×10.
5. Figured specimen. NMB D5867. Same specimen as Plate 2, figure 2. Calical surface, ×5.
6. Figured specimen. NMB D5763. Same specimen as Plate 2, figure 1. Transverse thin-section, ×10.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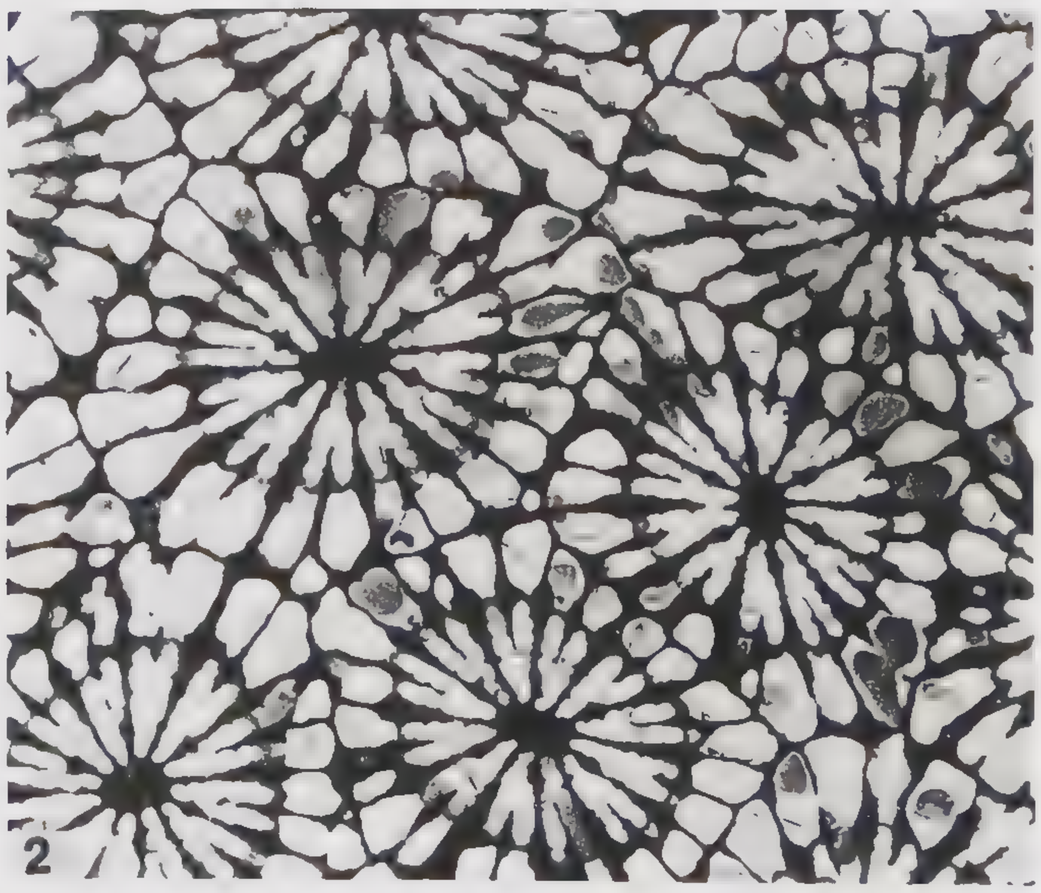
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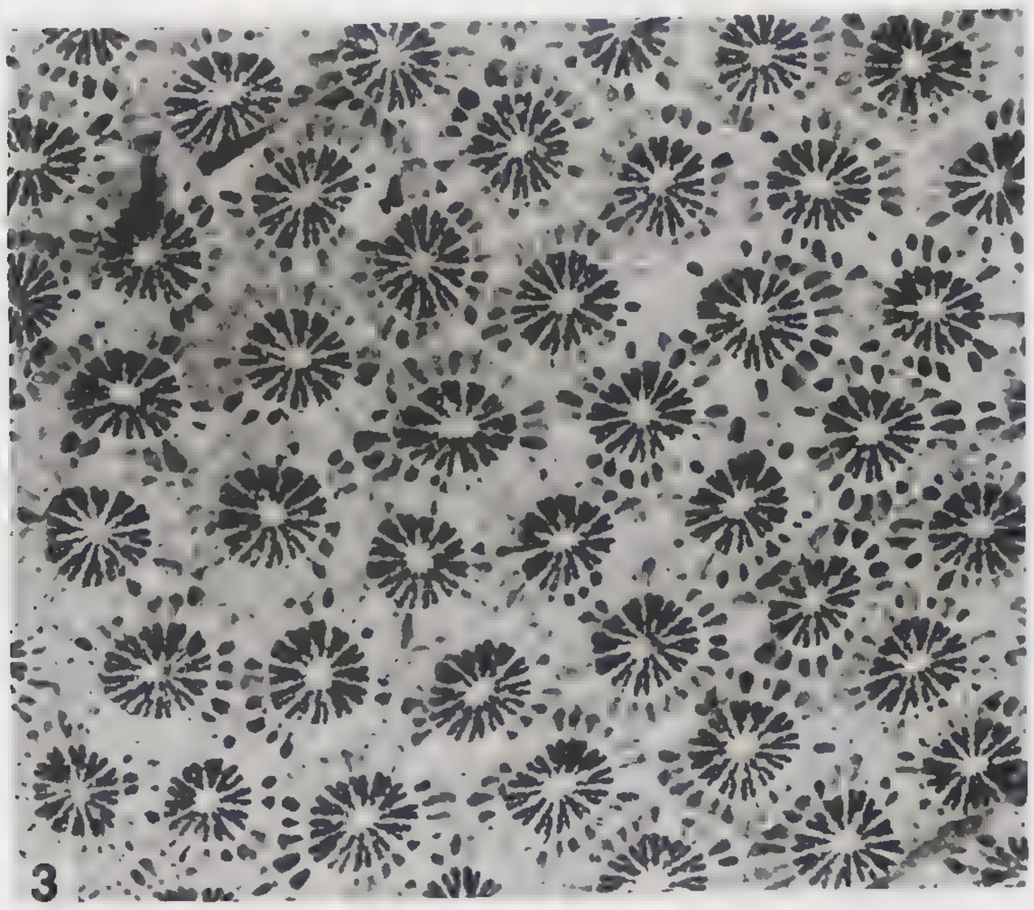
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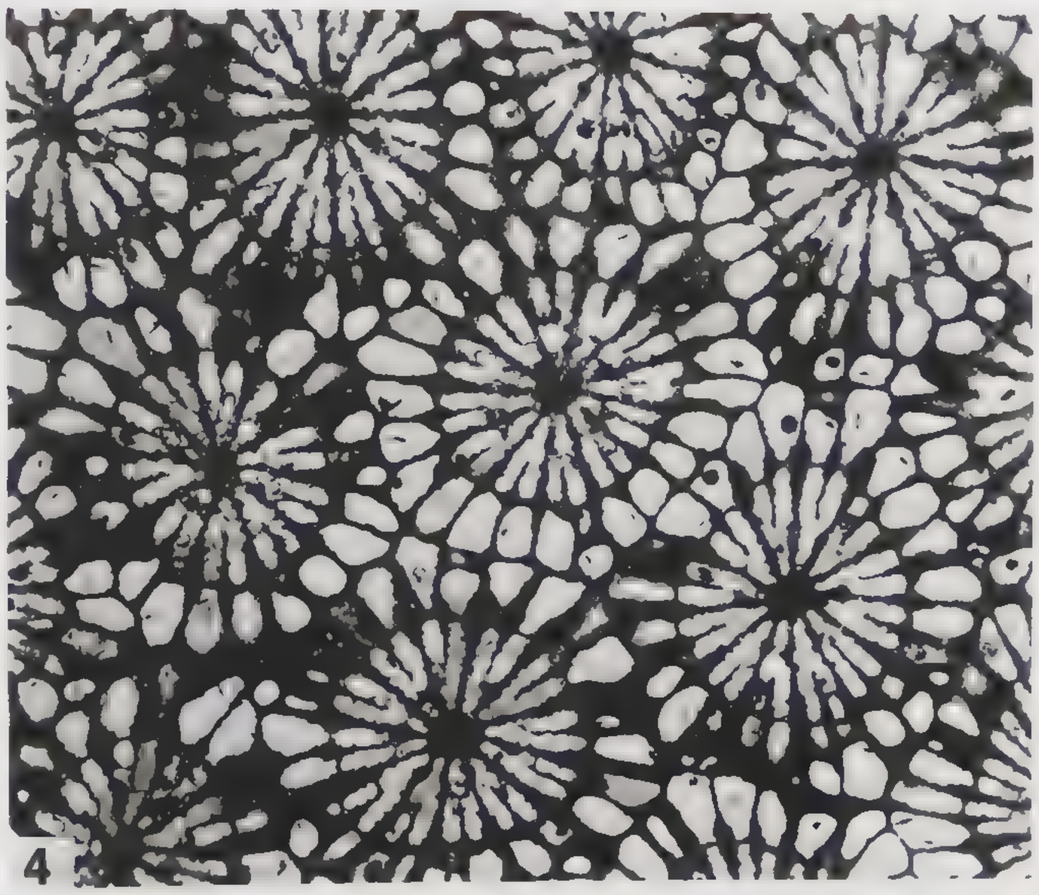
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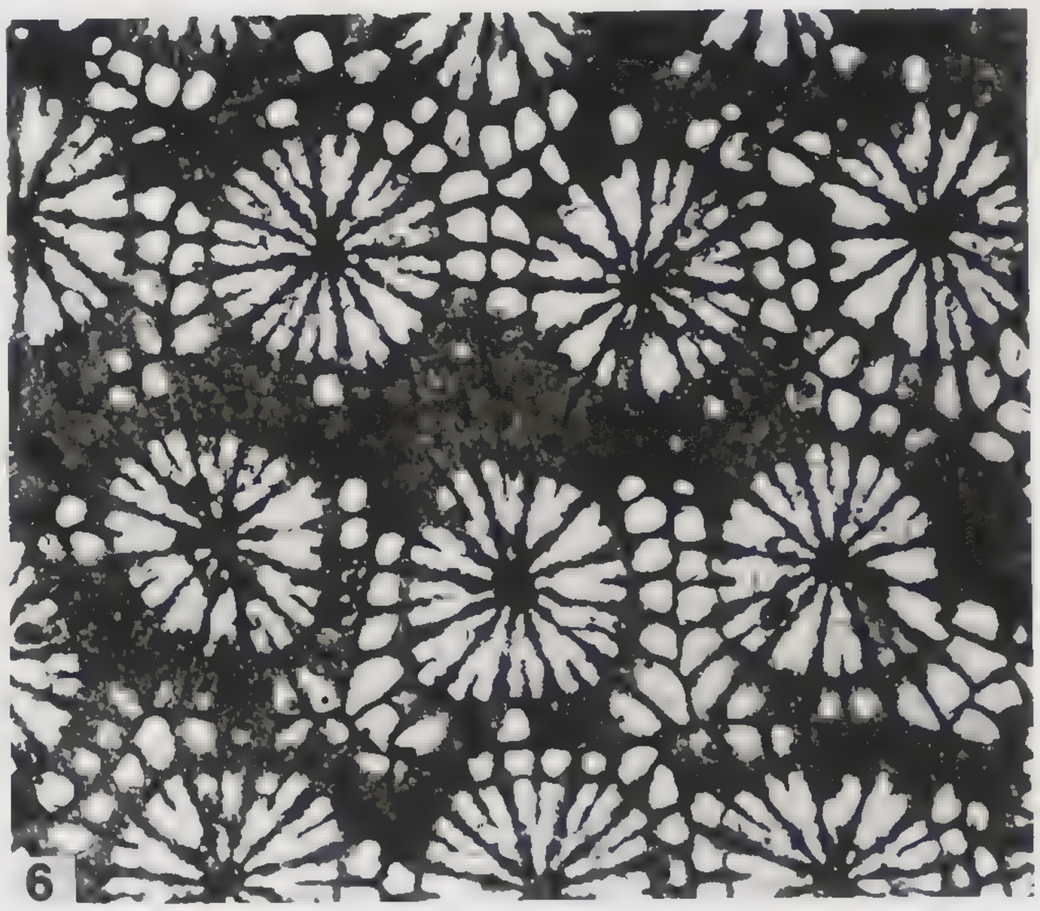
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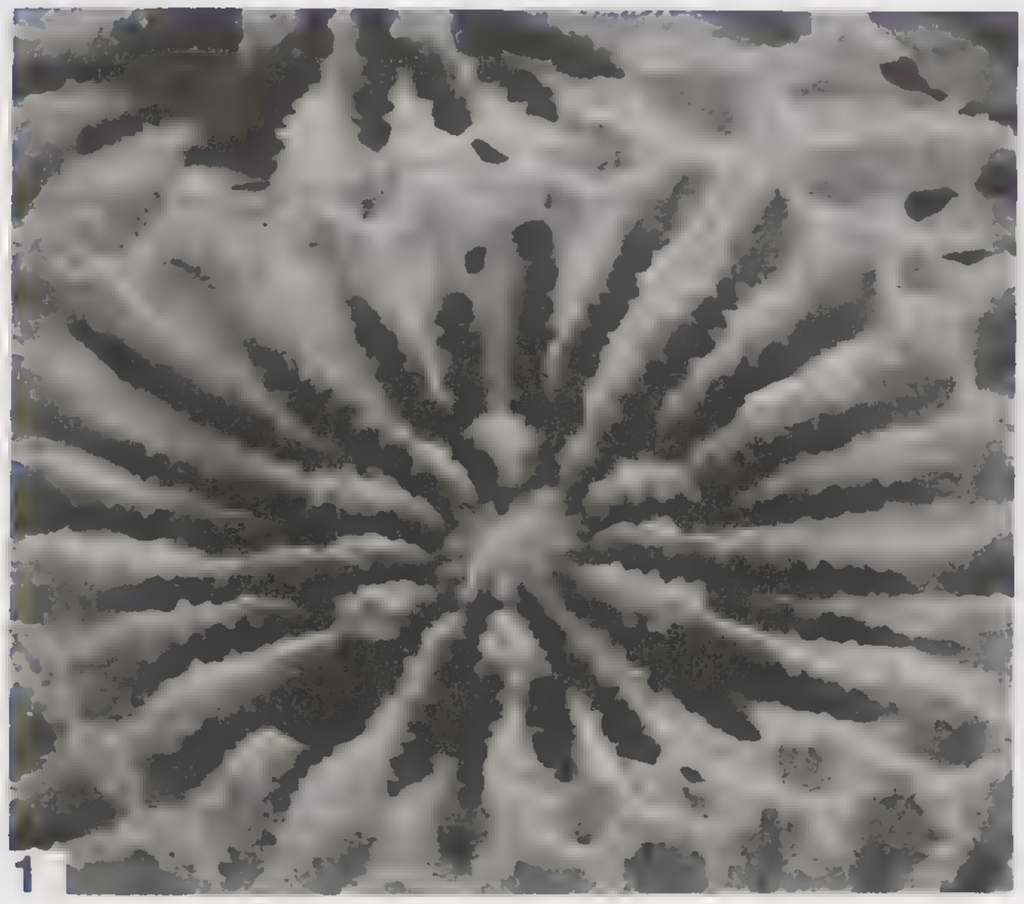
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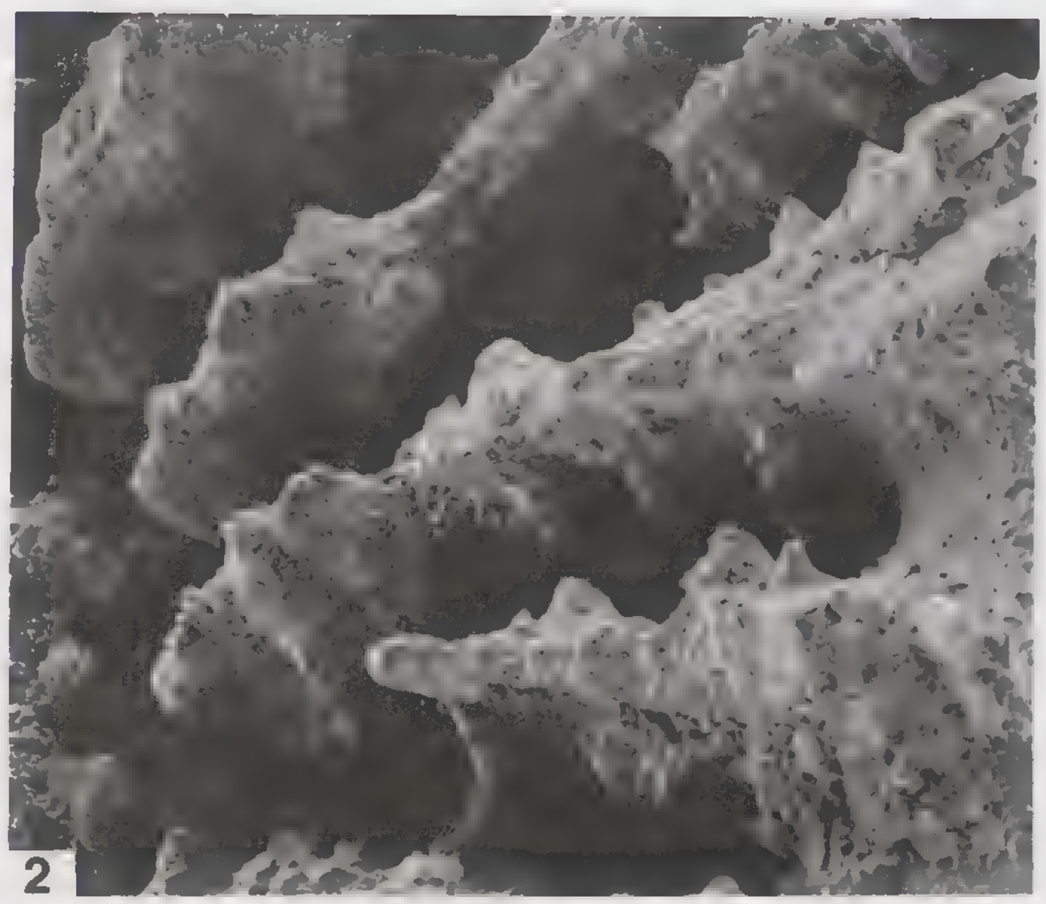
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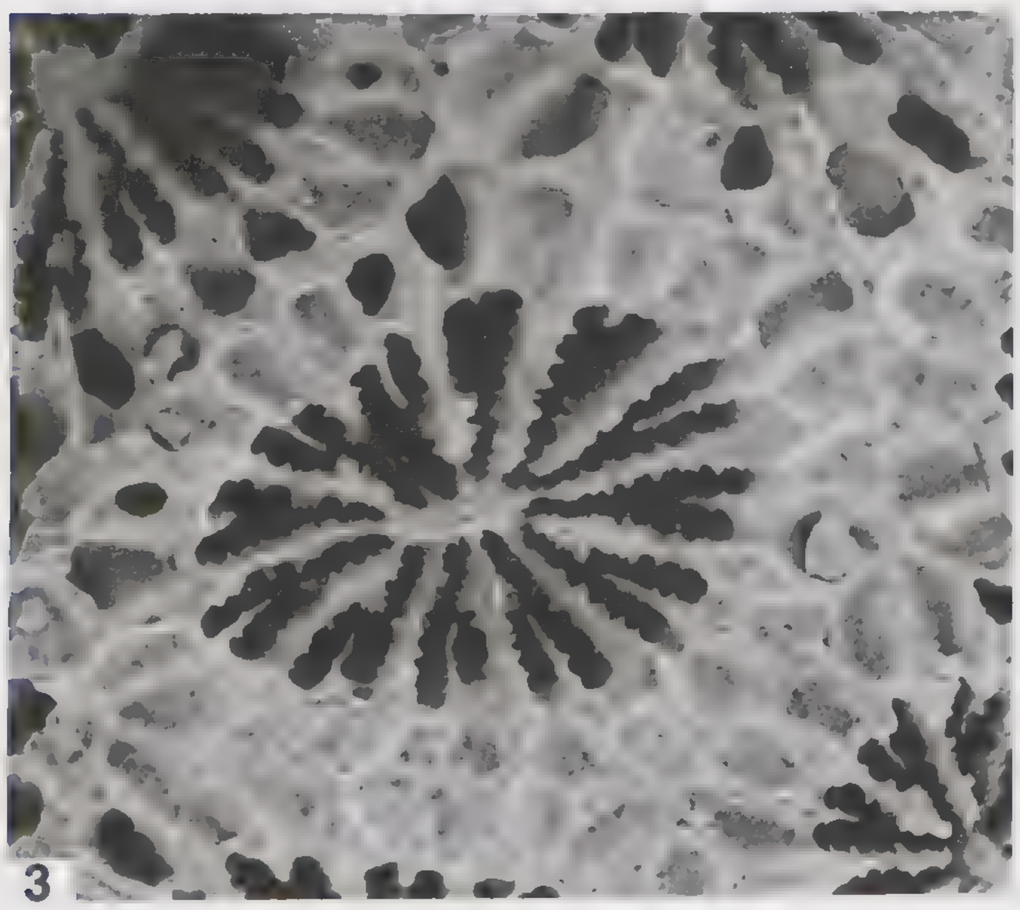
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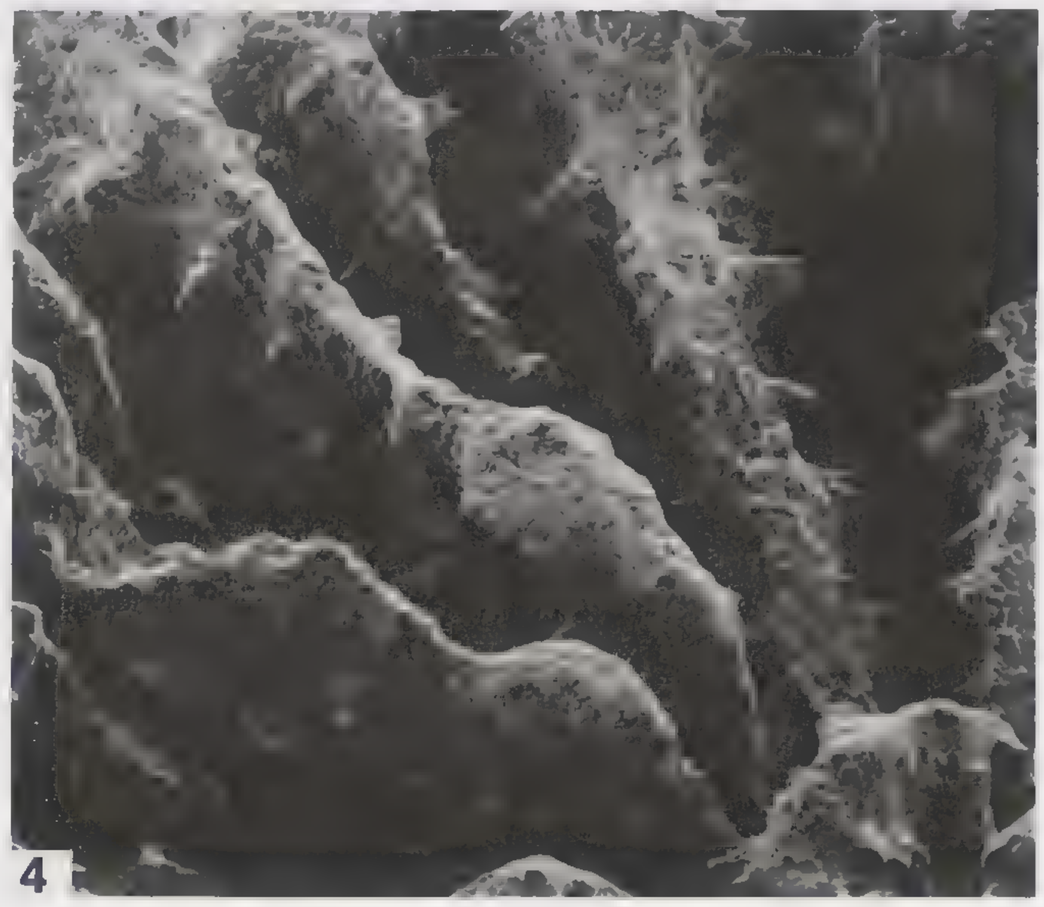
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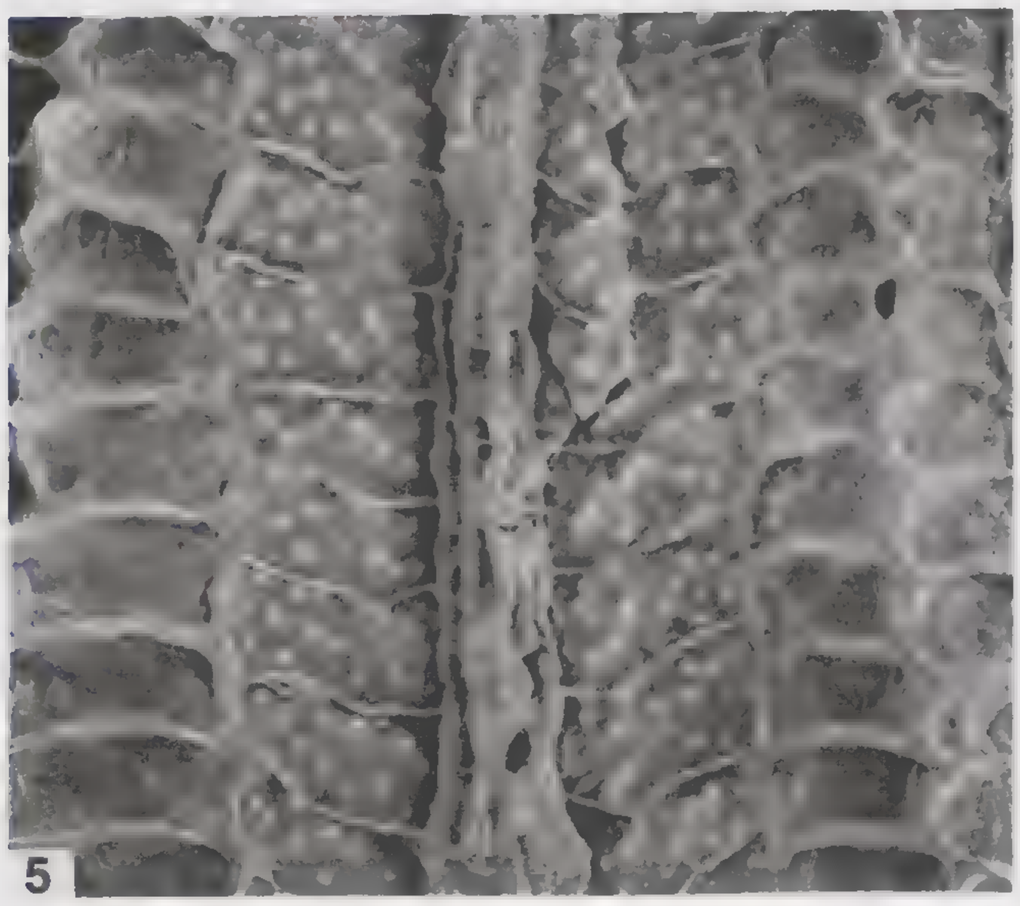
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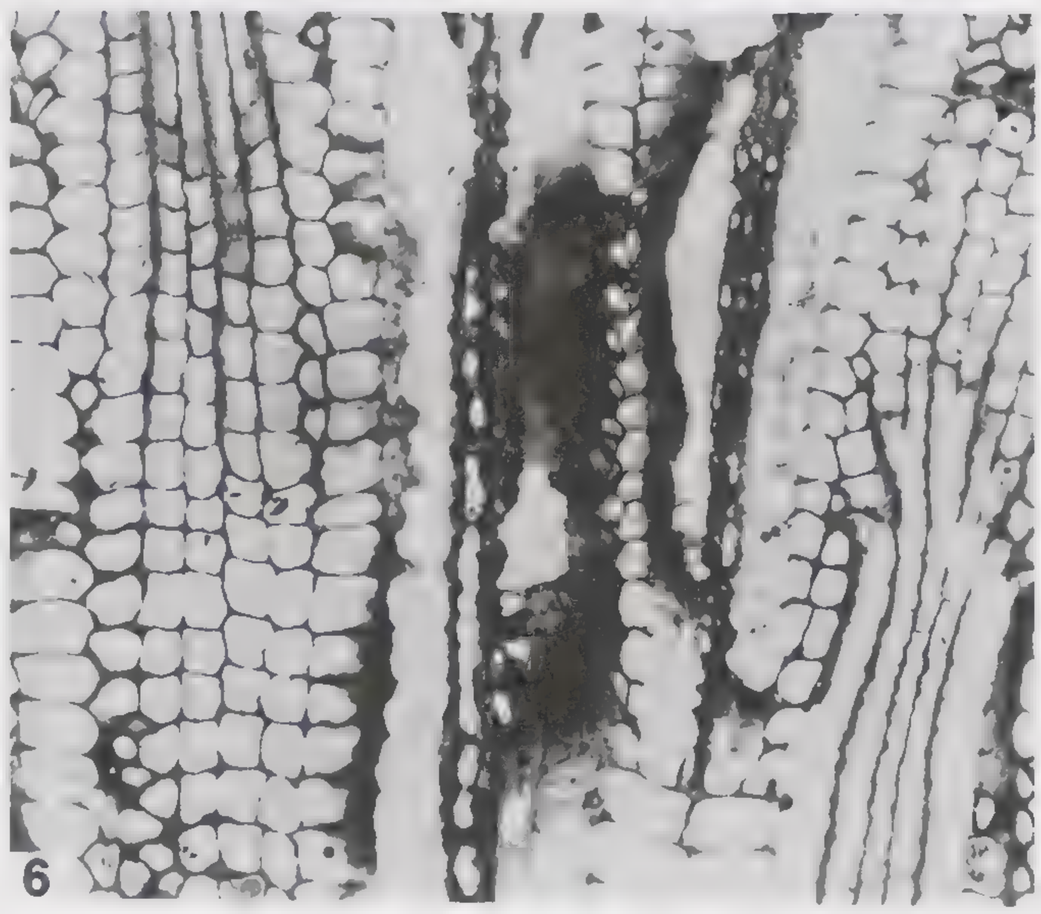
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EXPLANATION OF PLATE 4

Page

Stephanocoenia spongiformis (Duncan) 20

SEM photographs of calices and a broken longitudinal surface, and a photograph of a longitudinal thin-section. Vertical and horizontal skeletal structures are equally poorly developed. Septa are composed of six trabeculae that form moderate-sized surface denticles. The pali are elongate and consist of approximately three thickened trabeculae between the septa and columella. Endothecal dissepiments are especially weak, whereas exothecal dissepiments are better-developed with distinctly uniform spacing.

Figure

1. Figured specimen. NMB D5761. Same specimen as Plate 3, figure 2. Calical surface, ×20.
2. Figured specimen. NMB D5761. Same calice as figure 1 (left), showing columella, pali, and septa, ×100.
3. Figured specimen. NMB D5869. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×20.
4. Figured specimen. NMB D5869. Same calice as figure 3 (left) showing columella, pali, and septa, ×100.
5. Figured specimen. NMB D5761. Same specimen as figure 1 above showing a longitudinal break through a calice, ×20.
6. Figured specimen. NMB D5879. Upper Miocene, locality NMB 15850, Río Gurabo, Dominican Republic. Longitudinal thin-section, ×10.

EXPLANATION OF PLATE 5

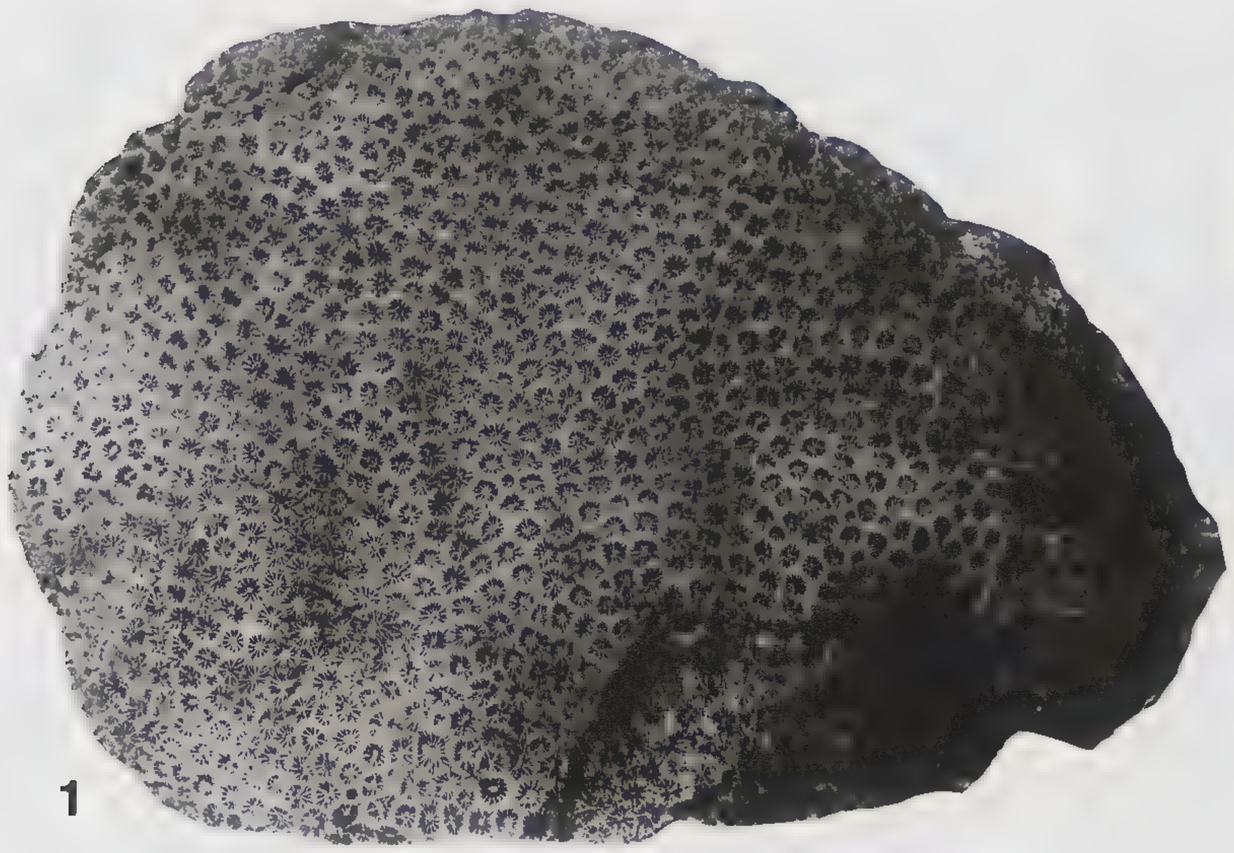
Page

Stephanocoenia duncani, new species 21

Whole colonies, closeups of calical surfaces, and X-radiographs. Some colonies are large with hemispherical shapes and a smooth outer surface. The calices are relatively large and polygonal, and the exothecal intercostal area weakly developed, if at all.

Figure

1. Paratype. NMB D5768. Lower Pliocene, locality NMB 16818, Río Cana, Gurabo Formation, Dominican Republic. Whole colony, ×½.
2. Holotype. NMB D5766. Lower Pliocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Whole colony, ×¼.
3. Paratype. NMB D5868. Upper Miocene, locality NMB 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Whole colony, ×¾.
4. Holotype. NMB D5766. Same specimen as figure 2 above. X-radiograph, ×½.
5. Holotype. NMB D5766. Same specimen as figure 2 above. Calical surface, ×5.
6. Holotype. NMB D5766. Same specimen as figure 2 above. Calical surface, ×5.



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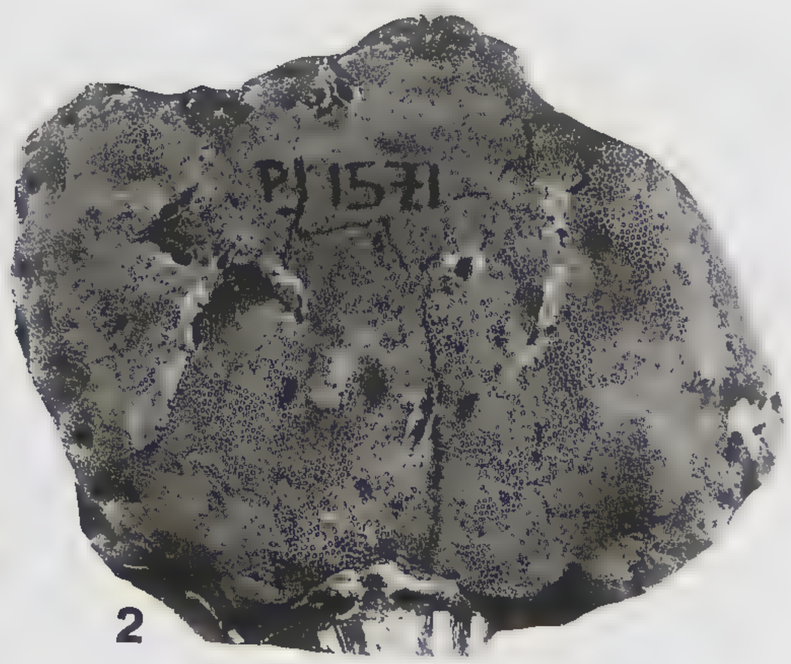

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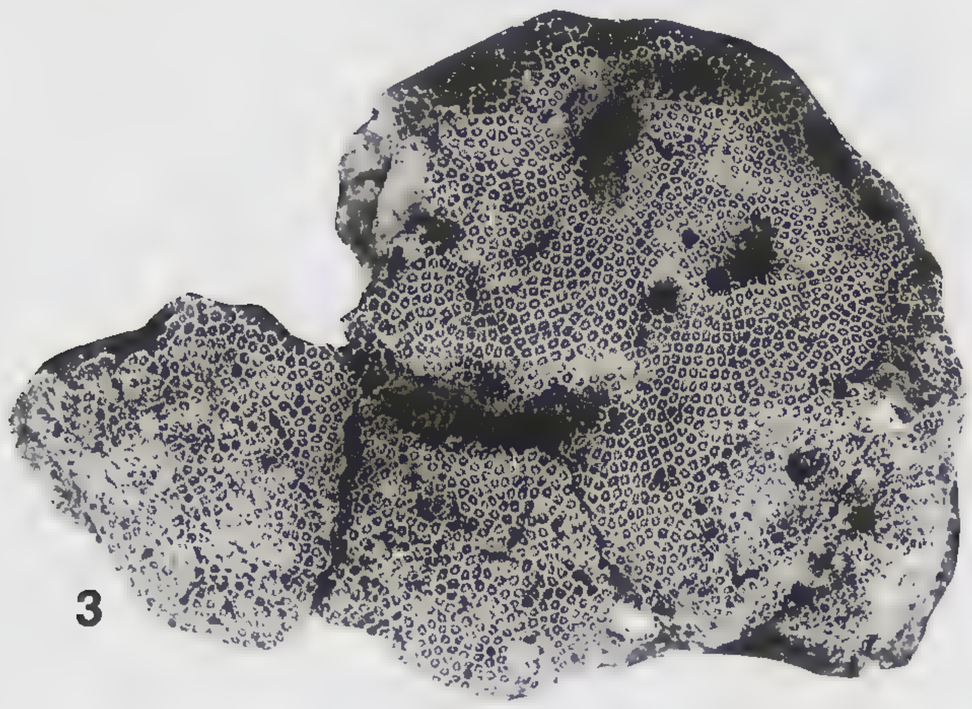

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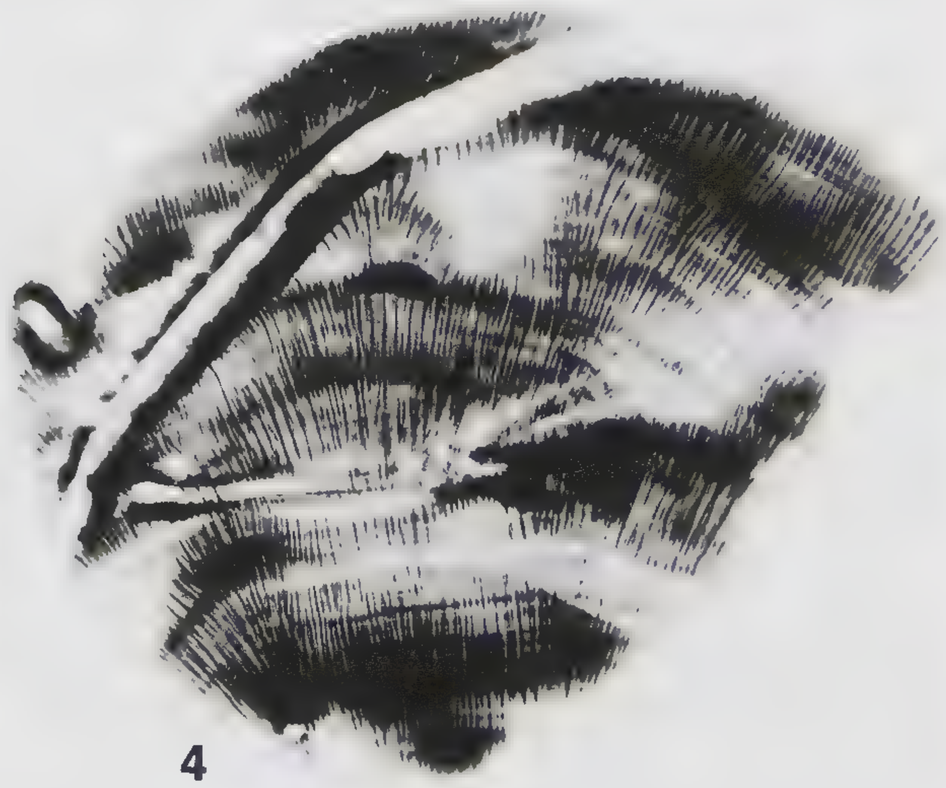

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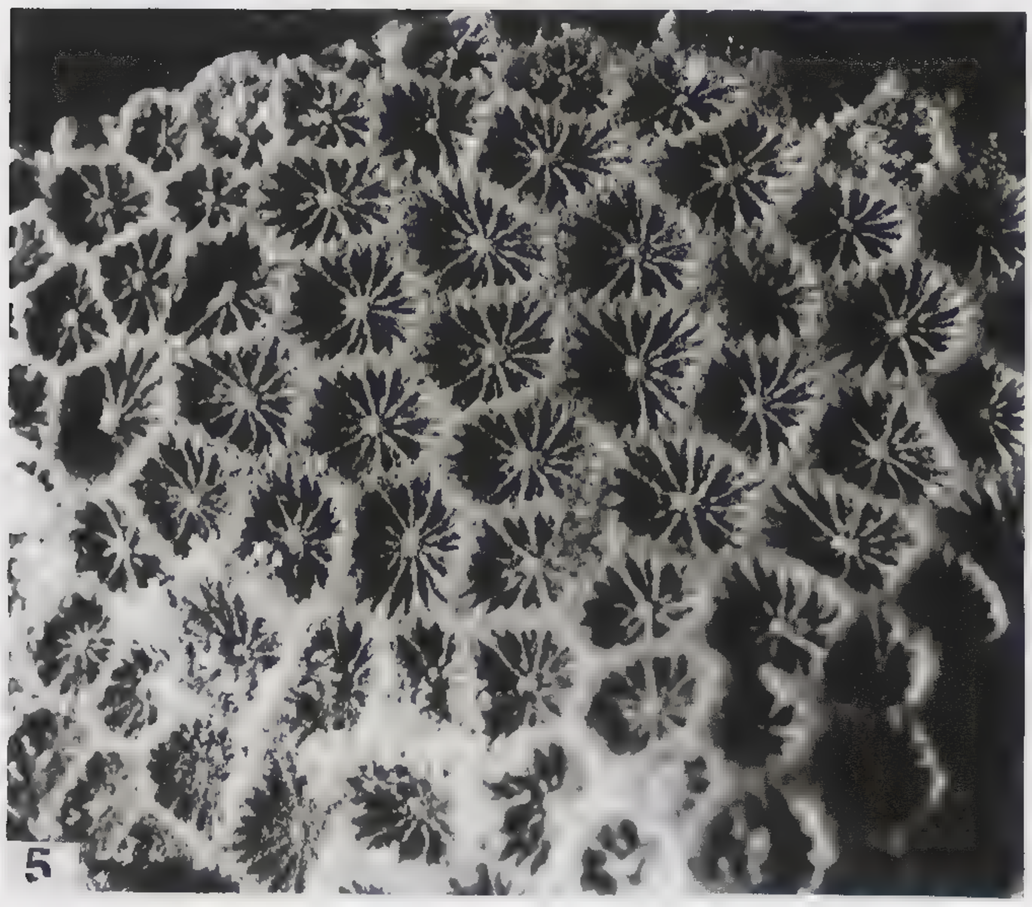

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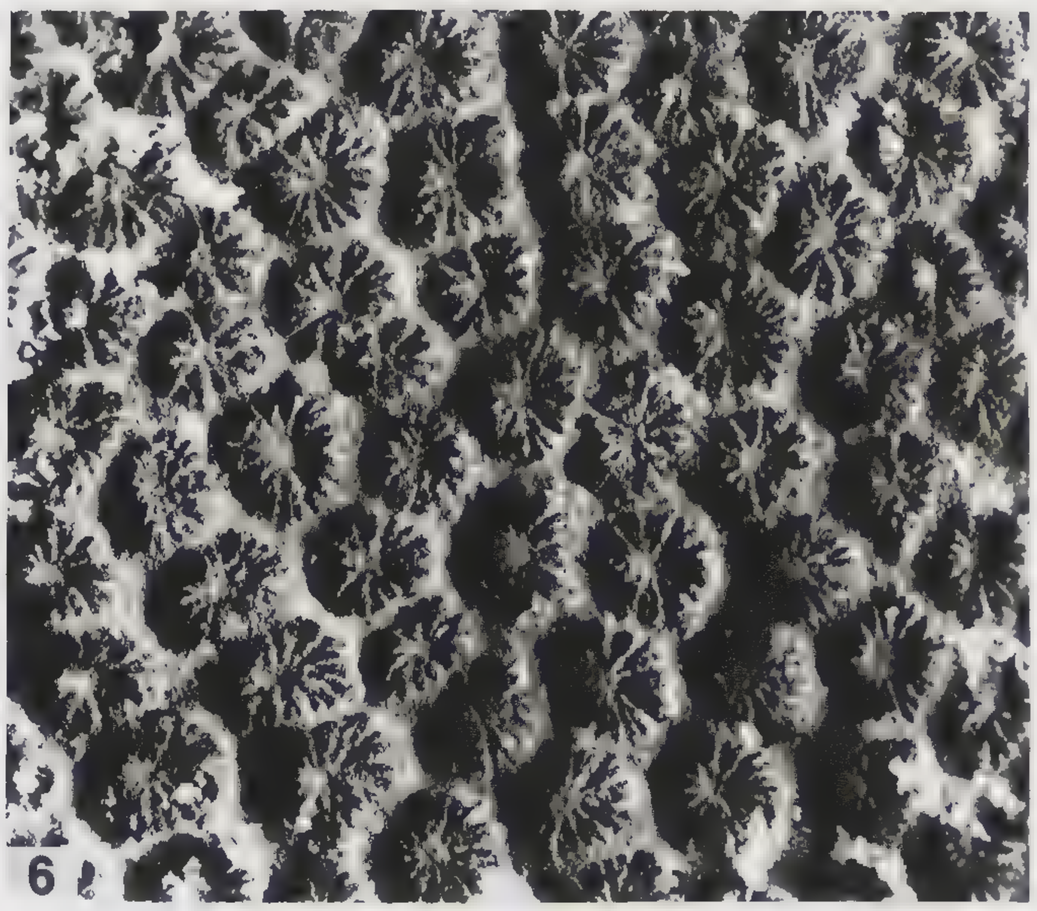

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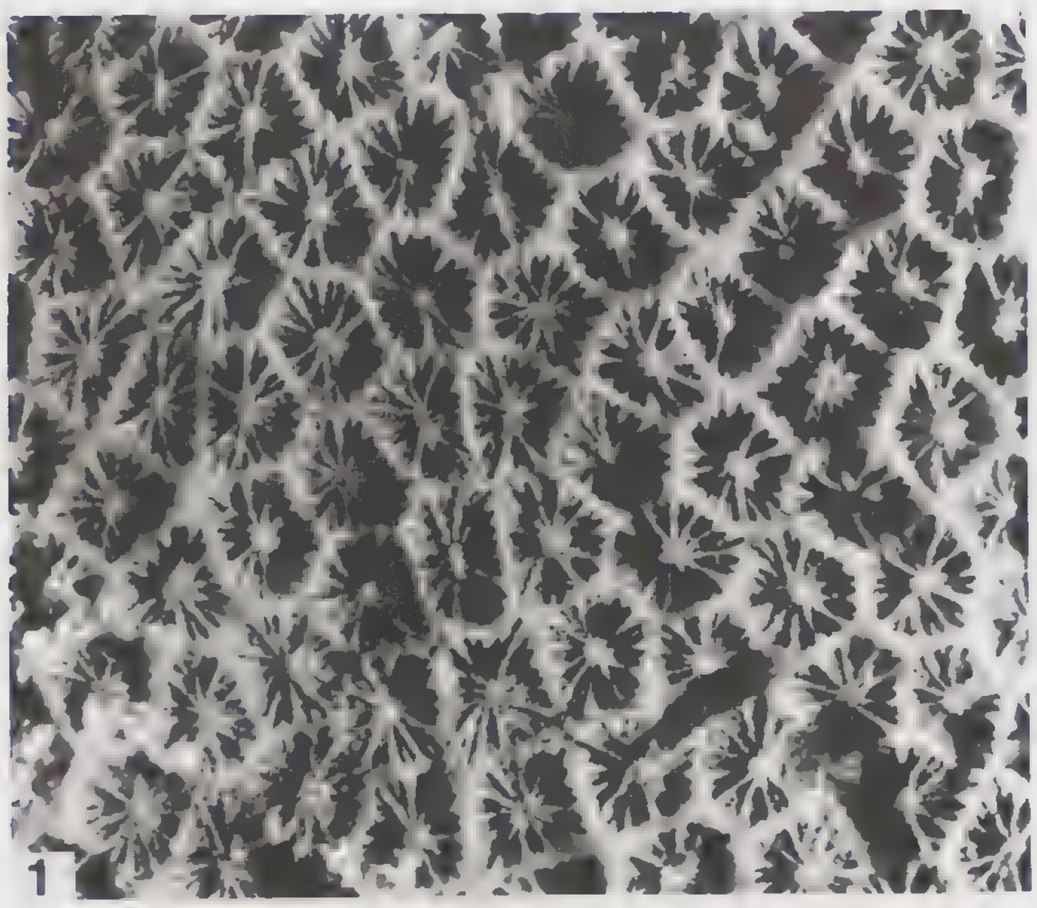
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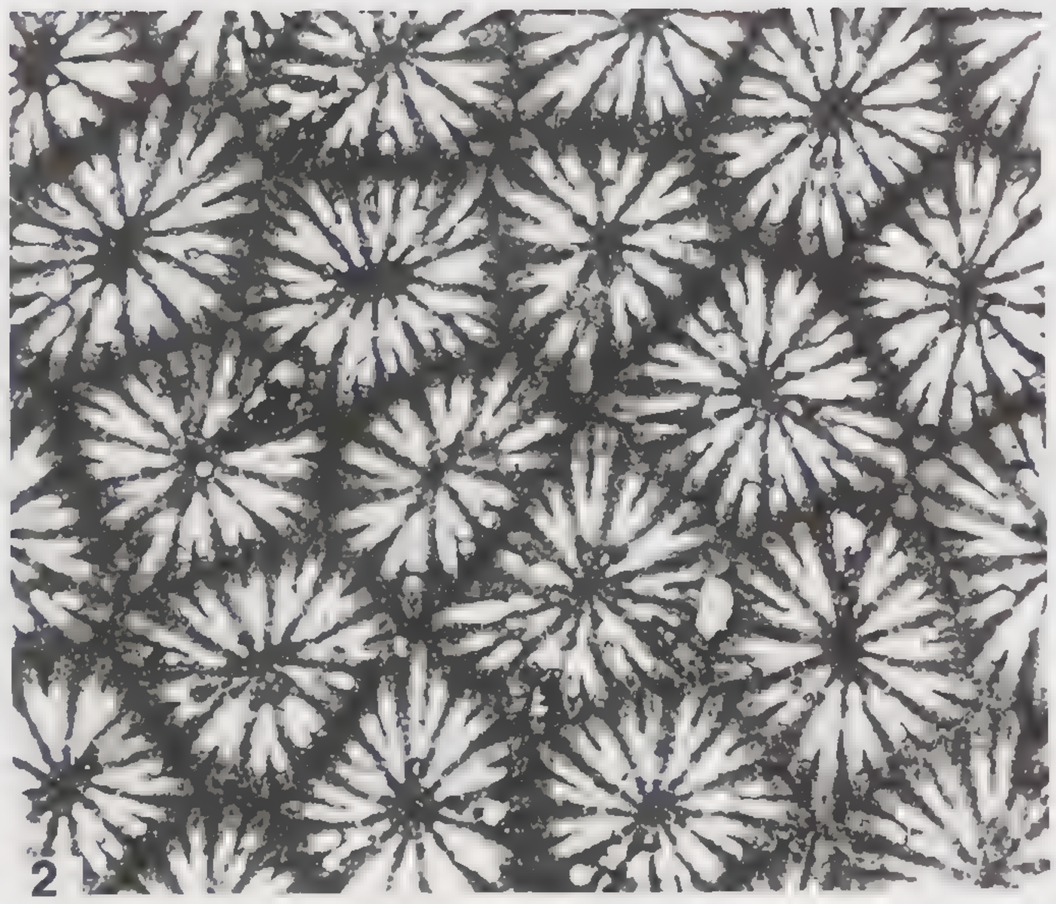
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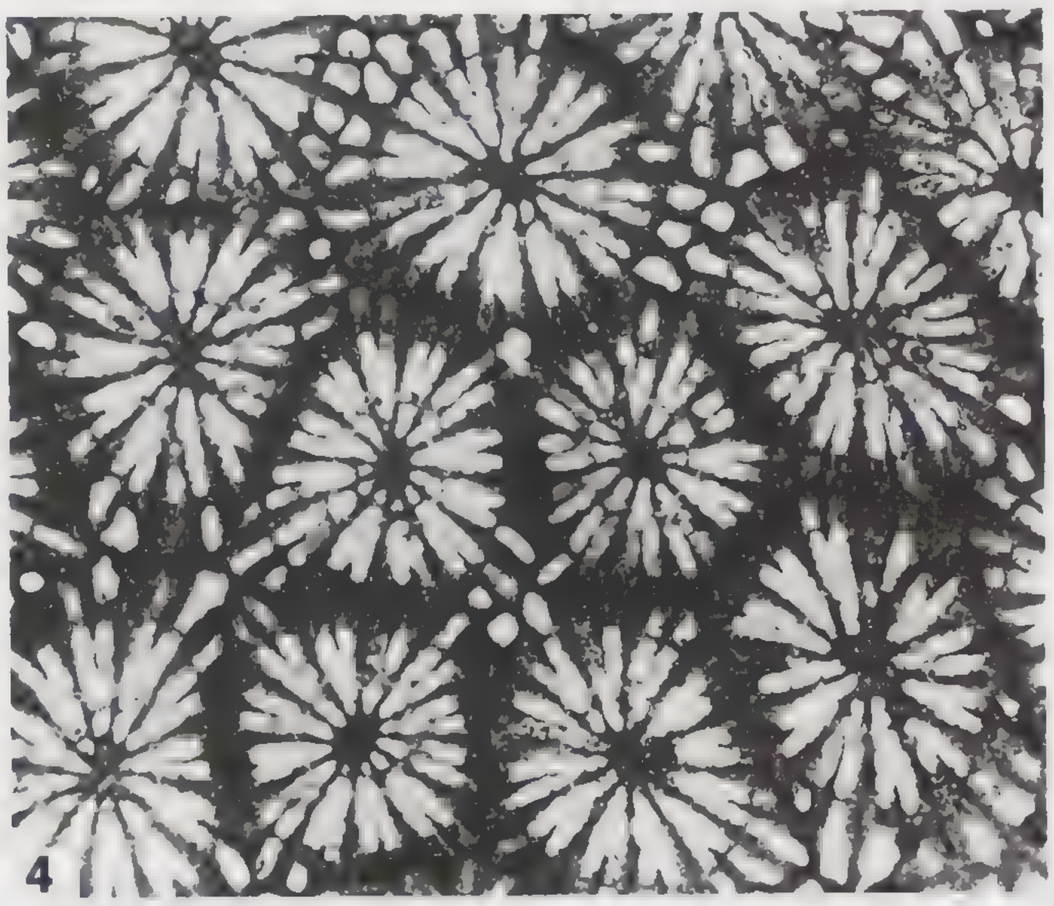
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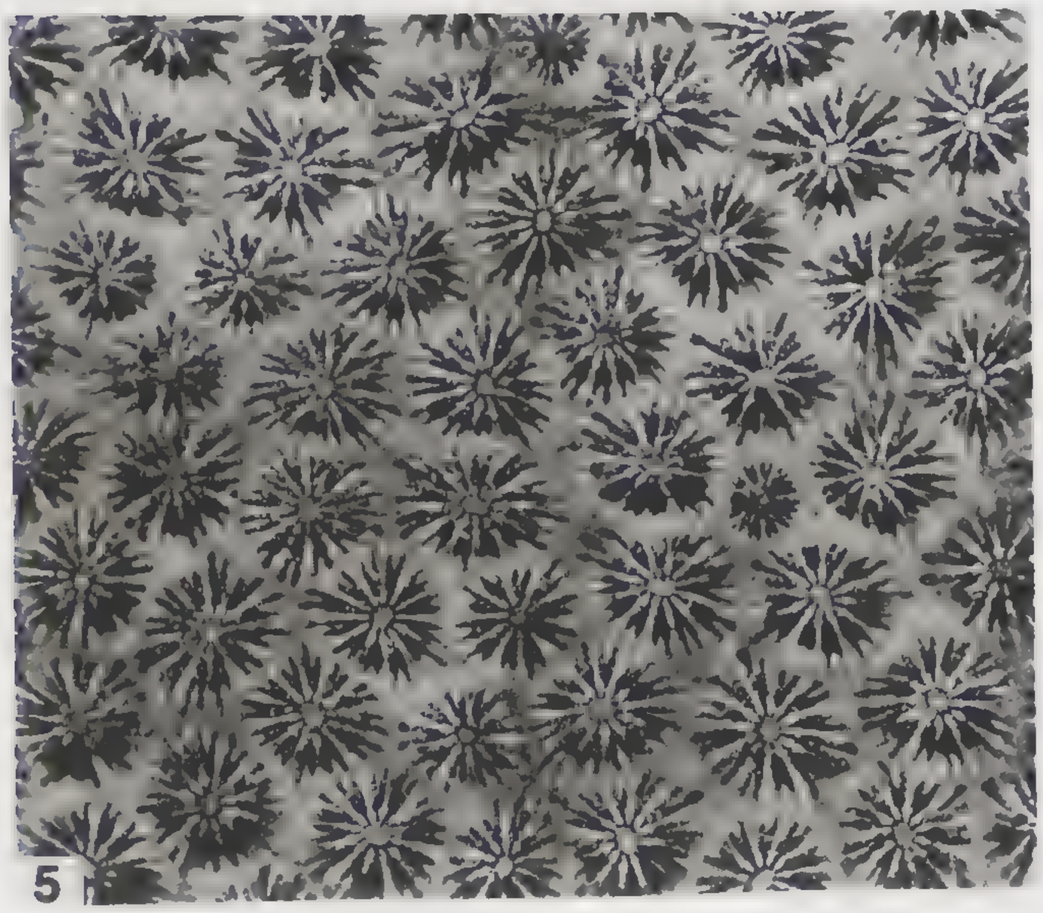
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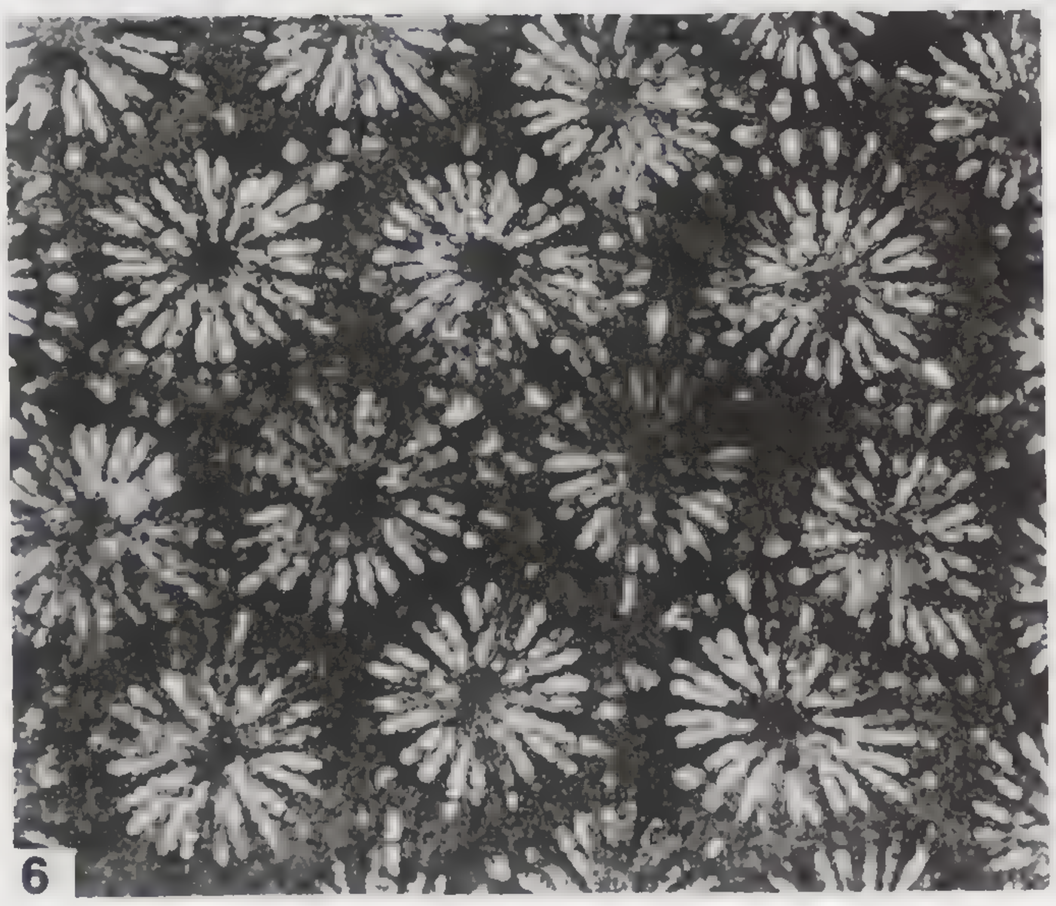
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EXPLANATION OF PLATE 6

Page

Stephanocoenia duncani, new species 21

Closeups of calical surfaces and transverse thin-sections. The corallites are roughly polygonal and closely-spaced and are separated by little or no pore space. The corallite walls are thick and dense. The pali are especially weak and the columella thick. Tertiary septa are relatively thick and short.

Figure

1. Paratype. NMB D5768. Same specimen as Plate 5, figure 1. Calical surface, ×5.
2. Paratype. NMB D5765. Lower Pliocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
3. Paratype. NMB D5769. Lower Pliocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Calical surface ×5.
4. Paratype. NMB D5871. Upper Miocene, locality NMB 16934, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
5. Paratype. NMB D5868. Same specimen as Plate 5, figure 3. Calical surface, ×5.
6. Paratype. NMB D5771. Lower Pliocene, locality NMB 16881, Río Cana, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.

EXPLANATION OF PLATE 7

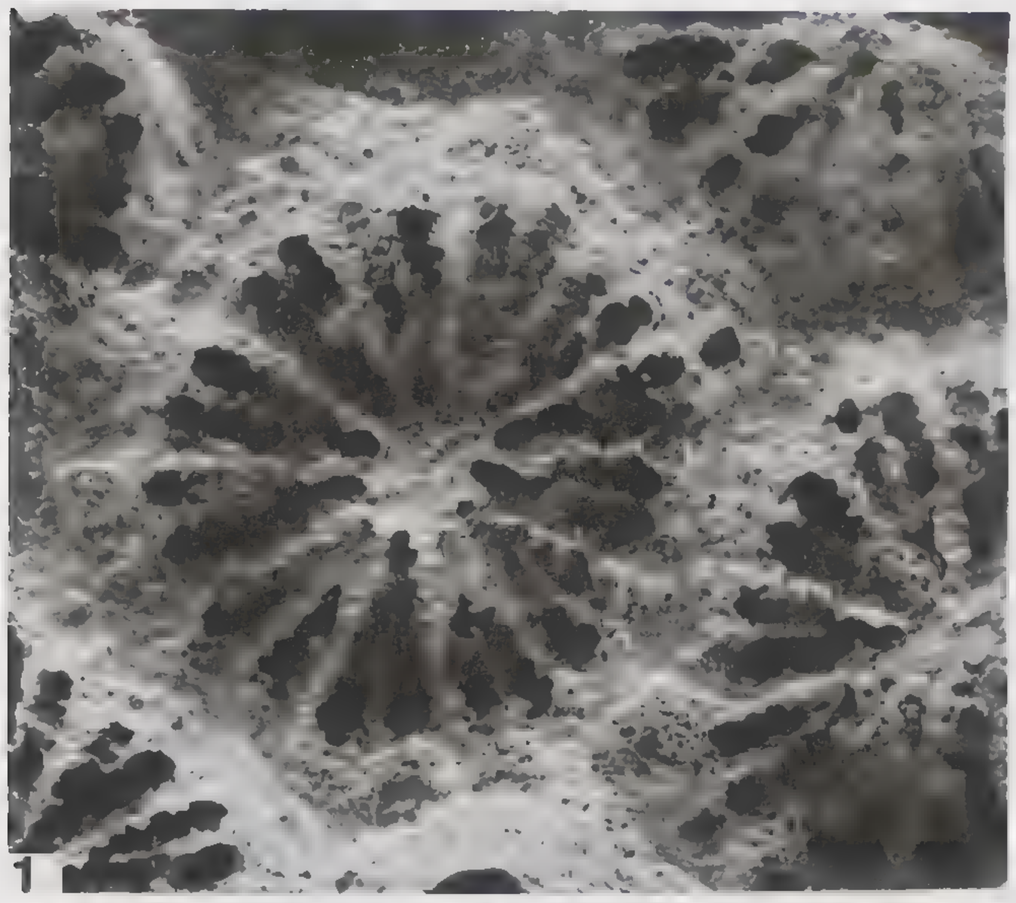
Page

Stephanocoenia duncani, new species 21

SEM photographs of calices and a broken longitudinal surface, and a photograph of a longitudinal thin-section. Vertical skeletal structures are generally less developed than horizontal ones. Septa are composed of five to six trabeculae that form minute surface denticles. The pali consist of two to three thickened trabeculae between the septa and columella. Endo- and exothecal dissepiments are thin and fairly regularly spaced.

Figure

1. Holotype. NMB D5766. Same specimen as Plate 5, figures 2, 4–6. Calical surface, ×20.
2. Holotype. NMB D5766. Same calice as figure 1 (above), showing columella, pali, and septa, ×100.
3. Paratype. NMB D5870. Upper Miocene, locality NMB 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×20.
4. Paratype. NMB D5870. Same calice as figure 3 (above), showing columella and pali, ×100.
5. Holotype. NMB D5766. Same specimen as figure 1 (above), showing a longitudinal break through a calice, ×20.
6. Paratype. NMB D5871. Same specimen as Plate 6, figure 4. Longitudinal thin-section, ×10.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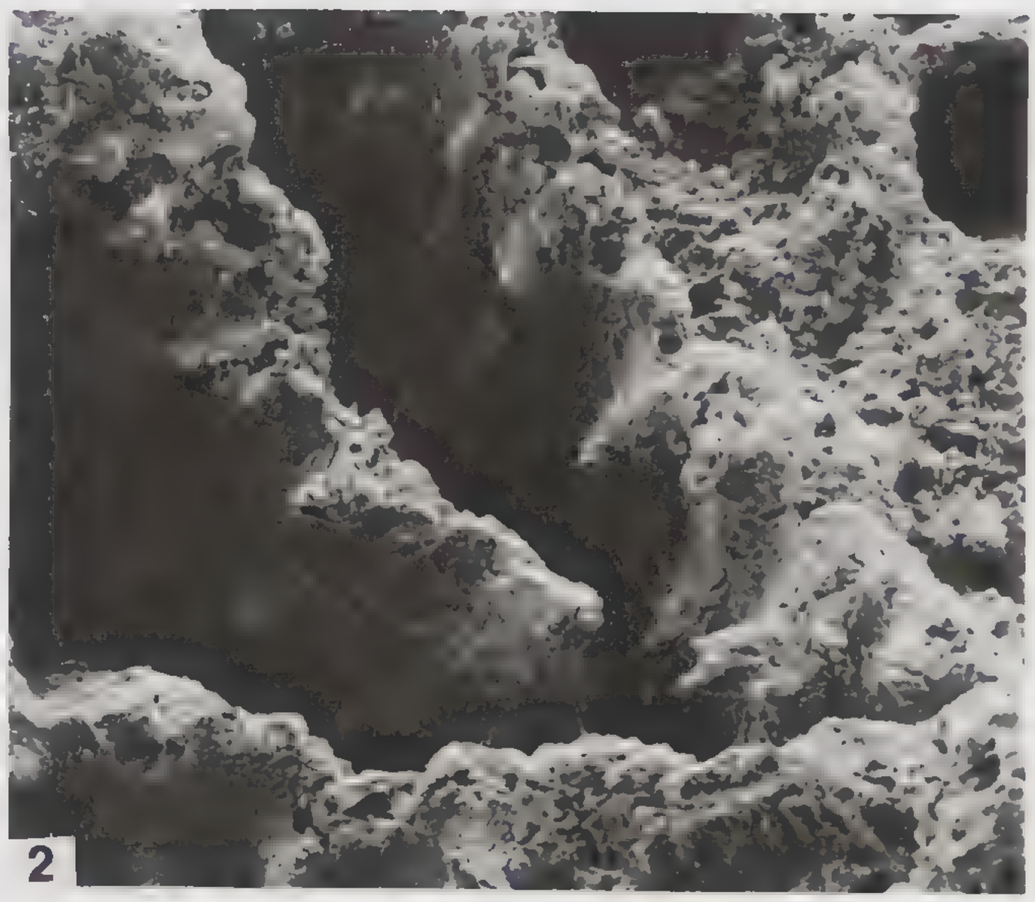
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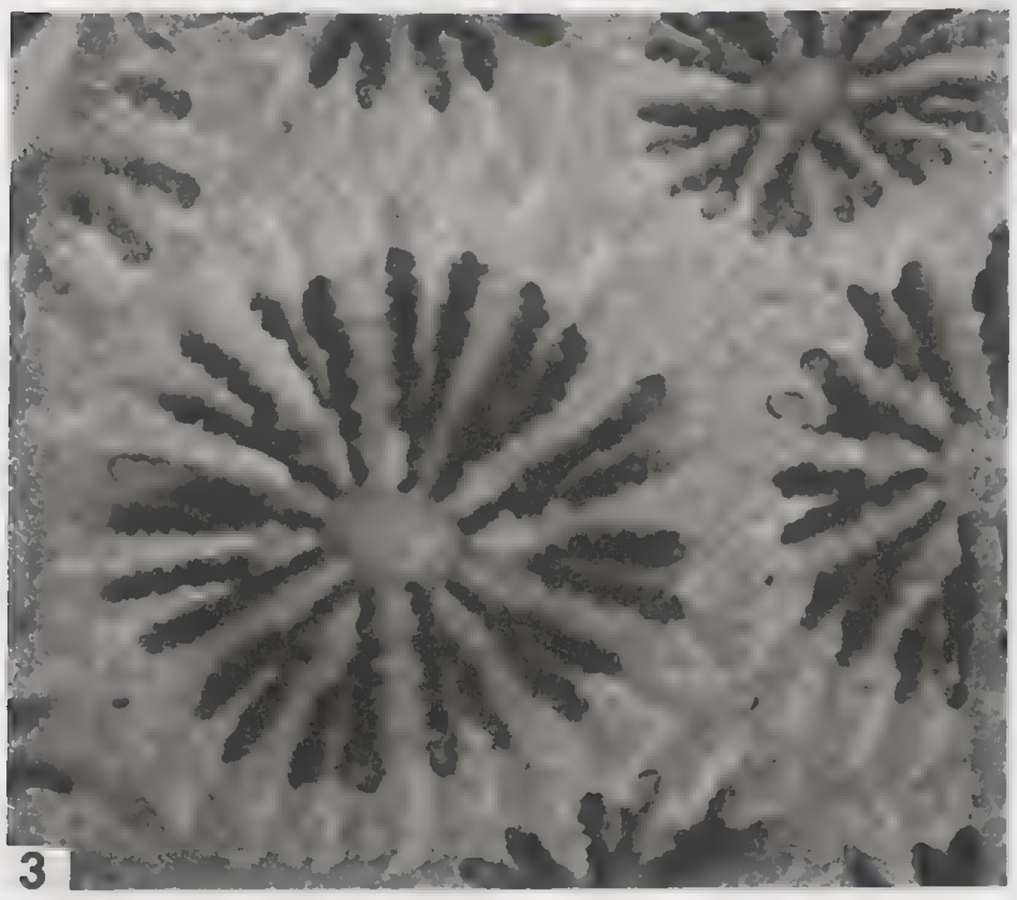
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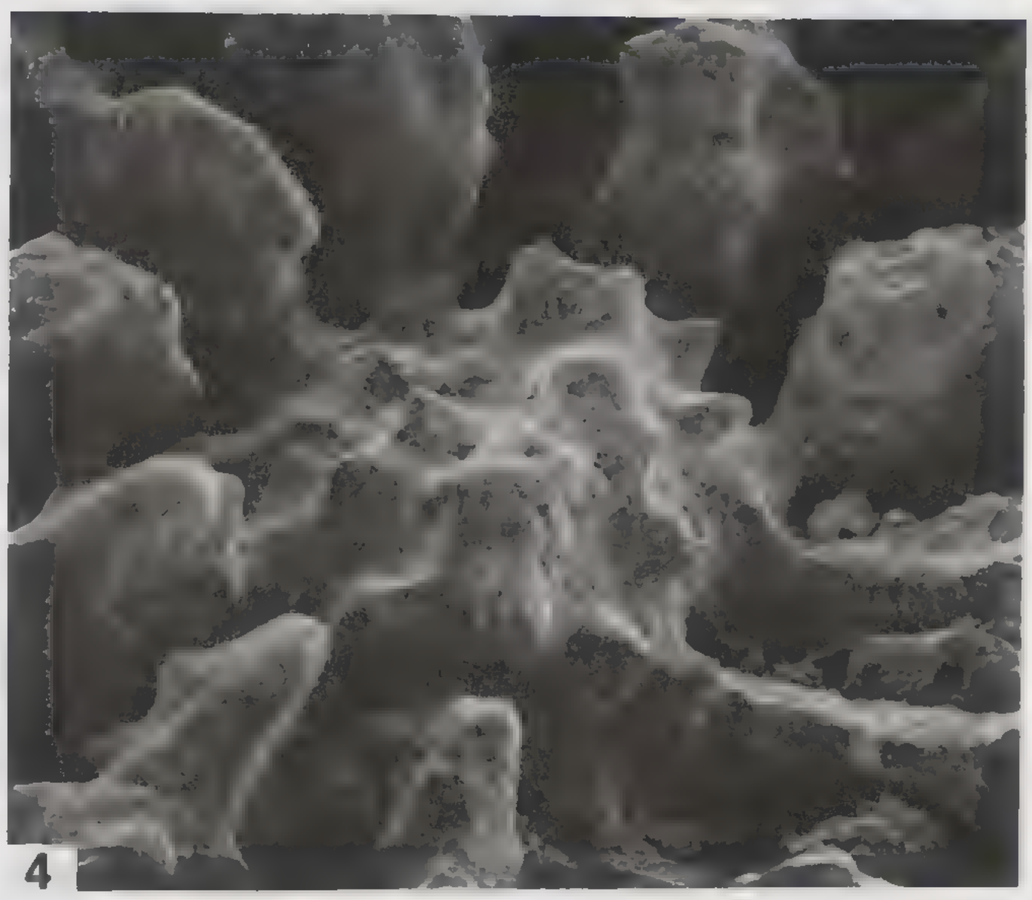
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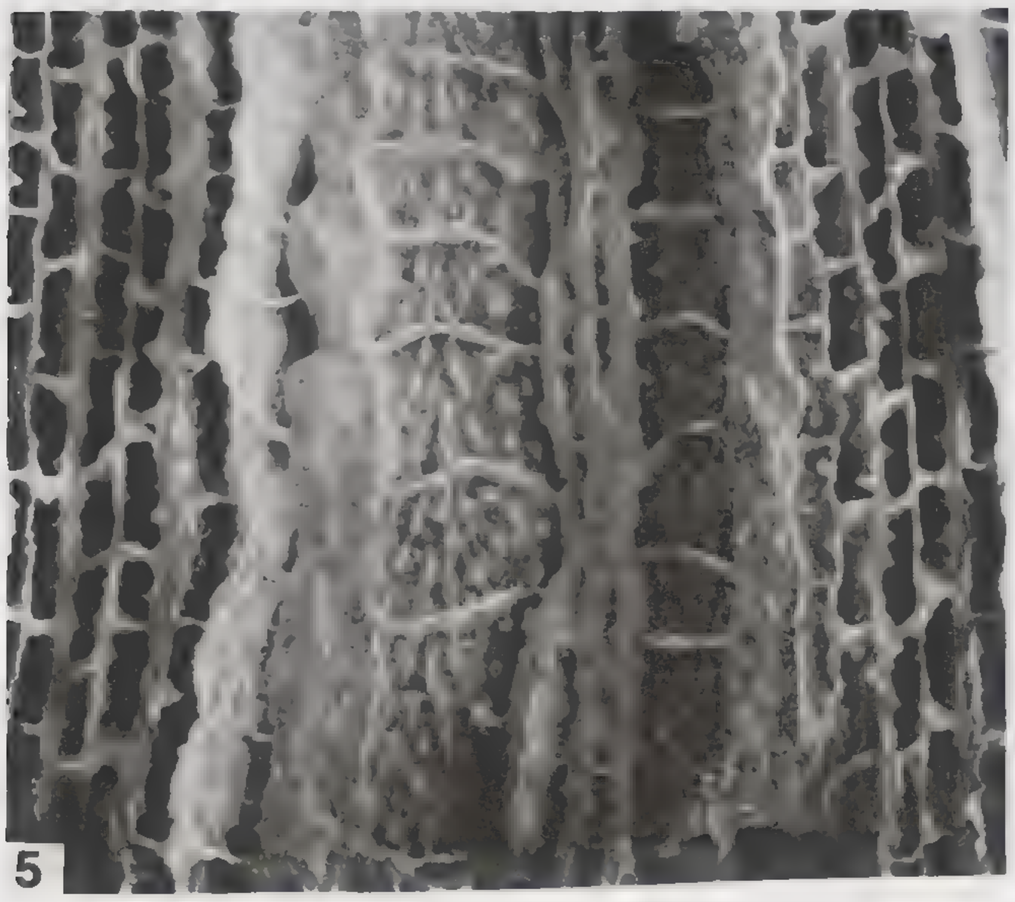
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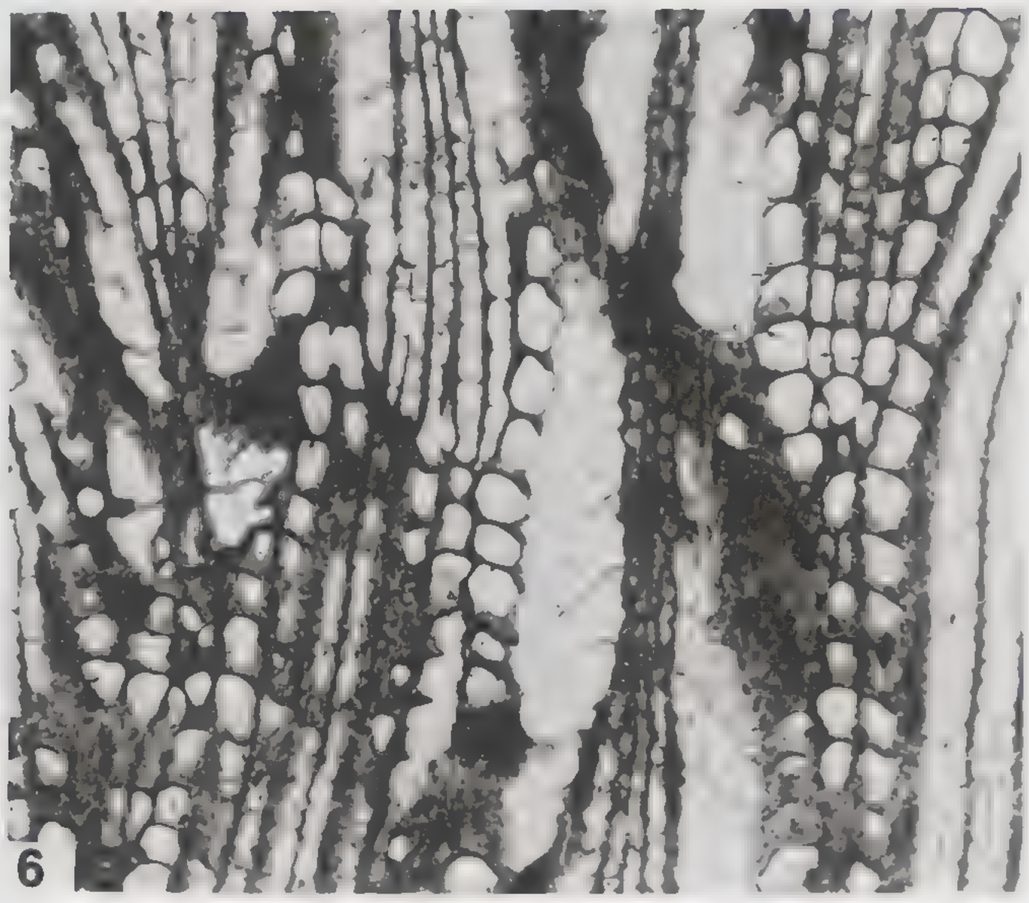
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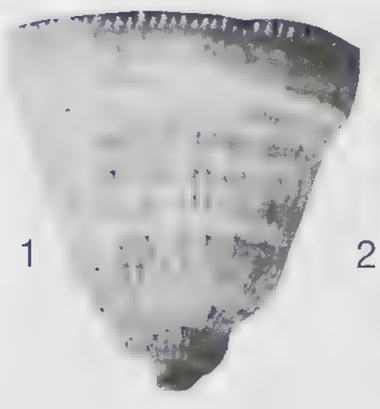

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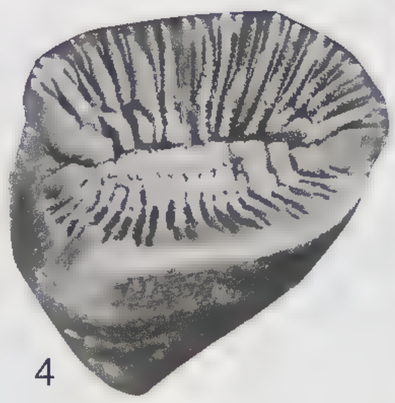

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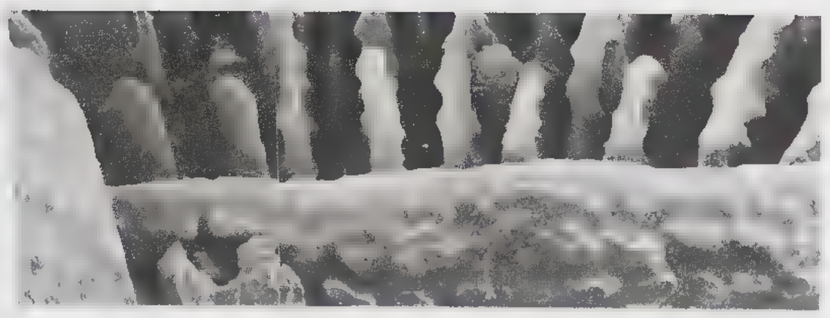

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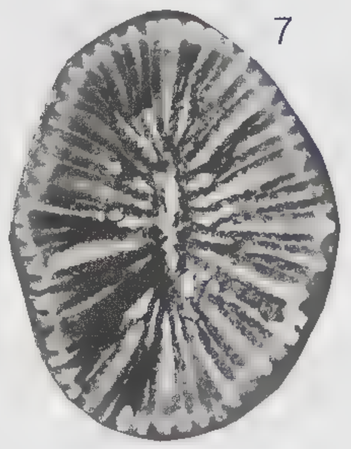

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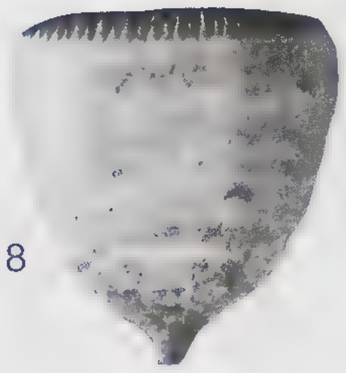

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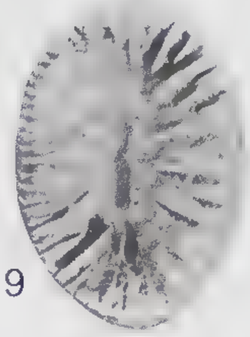

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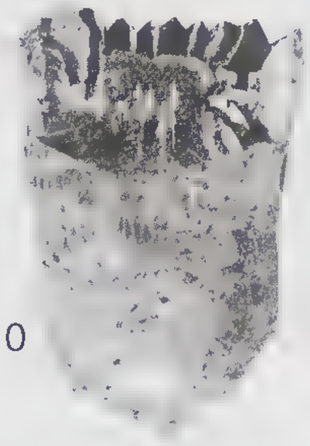

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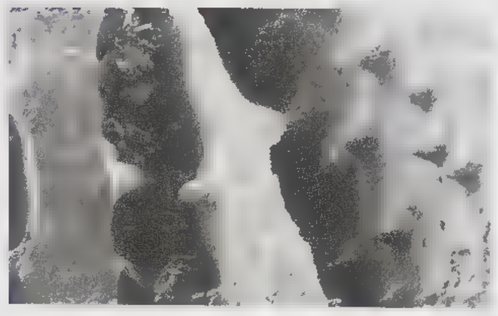

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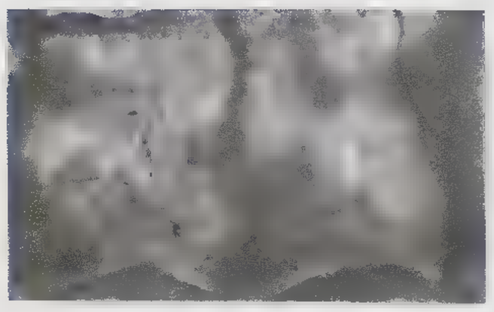

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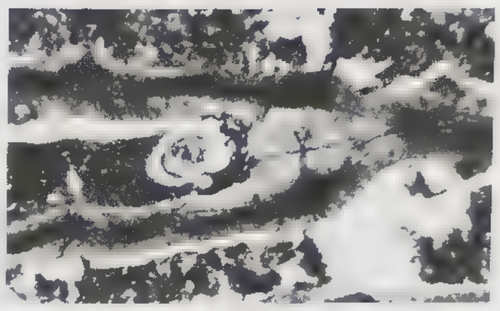

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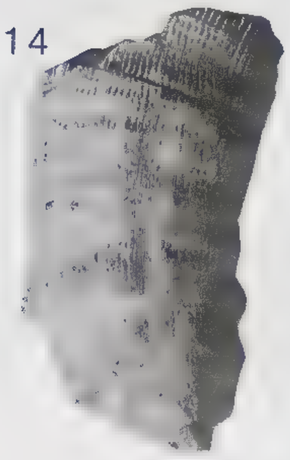

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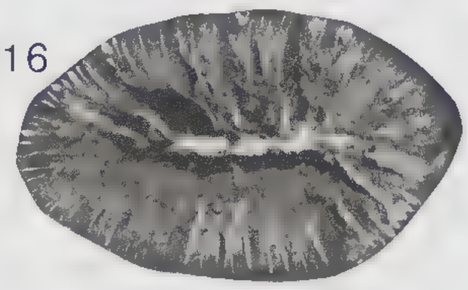

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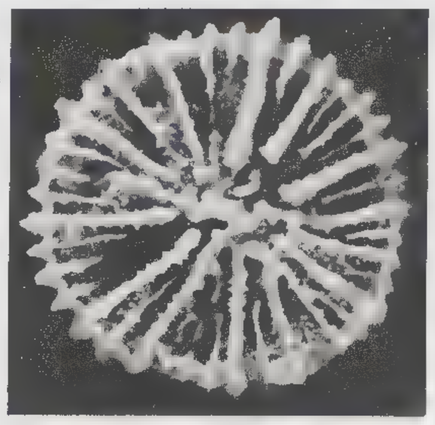

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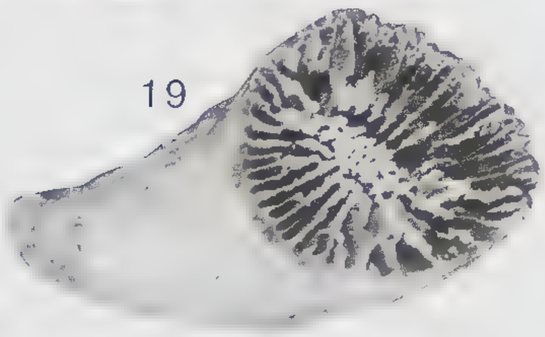

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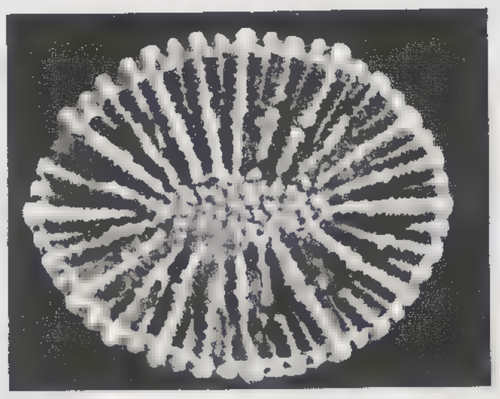

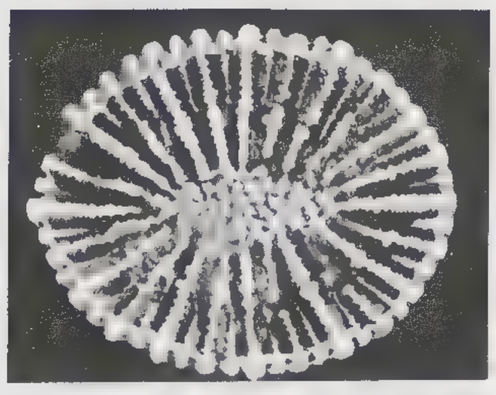

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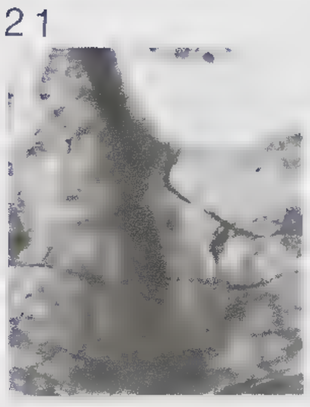

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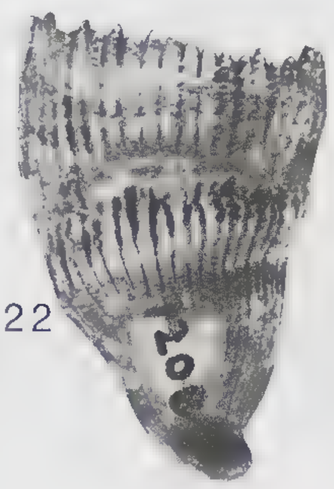

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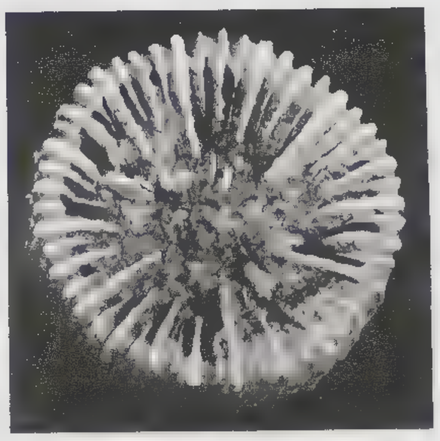
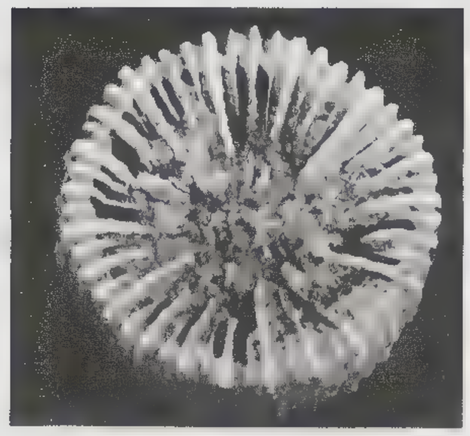




EXPLANATION OF PLATE 8

Figure — Page

1–7, 13. ***Antillocyathus maoensis*** (Vaughan, 1925) 28

1, 2. Side and calicular views of holotype (USNM 353644), ×2.0, ×2.1, respectively. Loc. USGS 7785.

3. Calice (NMB D5873) showing well-preserved pali and columella, ×2.2. Loc. NMB 15863.

4. Damaged calice (NMB D5874) showing well-preserved pali and columella, ×2.3. Loc. NMB 15864.

5. SEM of columella and pali (NMB D5875), ×9.8. Loc. NMB 15836.

6. Side view of upper calice (NMB D5876) showing degree of septal exsertness of primary septa, ×2.2. Loc. NMB 15863.

7. Aberrant paratype (MCZ 9267) with 58 septa, ×3.6. Loc. unknown.

13. Transverse thin-section through calice (NMB D5877) showing two septa joined to palus at right, ×19. Loc. NMB 15807.

8–12. ***Antillocyathus alatus***, new species 30

8, 9. Side and calicular views of holotype (NMB D5878), ×2.1, ×2.2, respectively. Loc. NMB 15871.

10. Paratype (NMB D5879) showing well-developed lateral costae, ×2.0. Loc. NMB 16857.

11. SEM of septal granules (NMB D5880), ×38. Loc. NMB 15962.

12. Transverse thin-section through calice (NMB D5881) showing theca and two septa, ×54. Loc. NMB 15863.

14–16. ***Antillocyathus cristatus*** (Vaughan, 1925) 30

14. Lateral face of large specimen (NMB D5882) showing lateral edge costae, ×0.85. Loc. NMB 15809.

15, 16. Side and calicular views of holotype (USNM 353643), ×1.4, ×1.6, respectively. Loc. USGS 7785.

17, 18. ***Paracyathus henekeni*** (Duncan, 1863) 34

Side and calicular views of lectotype [BM(NH) 28768], ×6.3, ×6.1, respectively. "Nivaje Shale".

19–21. ***Trochocyathus (Paratrochocyathus) chevalieri***, new species 31

19. Damaged calice of paratype (NMB D5883) showing pali and columella, ×2.0. Loc. NMB 15816.

20. Stereo view of calice of holotype (NMB D5884), ×3.4. Loc. NMB 15836.

21. Transverse thin-section of septal base (NMB D5885), ×86. Loc. NMB 15809.

22, 23. ***Trochocyathus (Paratrochocyathus) duncani***, new species 32

Side and calicular (stereo) views of holotype (USNM 74684), ×1.35, ×1.6, respectively. Loc. TU 1208.

EXPLANATION OF PLATE 9

Figure — Page

1, 2. ***Ceratotrochus* (*Edwardsotrochus*)** species cf. ***C.* (*E.*) *duodecimcostatus*** (Goldfuss, 1826) 33
Side and calicular views of specimen from Loc. NMB 15836 (NMB D5886), ×1.35, ×1.5, respectively.

3, 4. ***Ceratotrochus* (*E.*) *duodecimcostatus*** (Goldfuss, 1826) 33
Side and calicular views of specimen from Rio Torsero, Italy (Pliocene) (USNM 326663), ×1.3, ×1.4, respectively.

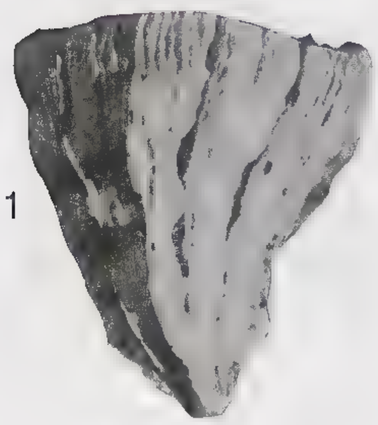
5–9. ***Paracyathus sinuosus***, new species 34
5. SEM of damaged calice of paratype (NMB D5887) showing septal granules and paliform lobes, ×8.9. Loc. NMB 15833.
6, 7. Side and calicular views of holotype (NMB D5888), ×5.0, ×6.9, respectively. Loc. NMB 15833.
8. SEM of upper theca (NMB D5887) showing sinuous costae, ×20.3. Loc. NMB 15833.
9. Transverse thin-section of calice (NMB D5890) showing wall and two septa, ×67. Loc. NMB 15833.

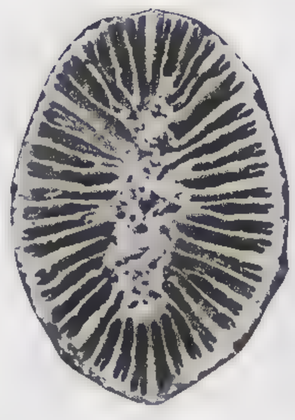
10–12. ***Deltocyathus italicus*** (Michelotti, 1838) 35
10, 11. Calicular and basal views of single specimen from Dominican Republic (USNM 63125), ×3.9. Loc. USGS 8702.
12. Basal view of specimen from the Miocene of Tortona, Italy (MNHNP L 60), ×3.35.

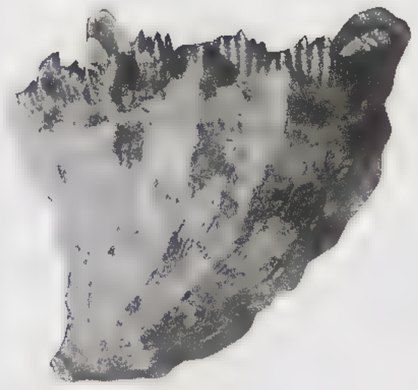
13. ***Deltocyathus*** species cf. ***D. italicus*** (Michelotti, 1838) 35
Basal view of Recent specimen (USNM 36443), ×3.3, U.S. Fish commission Steamer *Albatross* sta. 2751: 22°41′N, 84°17′W, 772 m, 21 Jan. 1885.

14–19. ***Sphenotrochus* (*Eusthenotrochus*) *senni*** Wells, 1945 36
14–17. SEM of specimen (NMB D5891) from Loc. NMB 16938.
14, 15. Side and calicular views, ×8.6, ×10.9, respectively.
16. Elongate costae in lower third of lateral face of corallum, ×25.3.
17. Costal granulation near upper thecal edge, each costa composed of two rows of granules, ×23.5.
18. Holotype (USNM 68358) from Martinique, ×3.9.
19. Lateral face of specimen (NMB D5892) from Loc. NMB 15900, ×4.4.

20, 21. ***Dominicotrochus dominicensis*** (Vaughan, 1925) 36
Side and calicular views of a specimen (USNM 68359) reported by Wells (1945) from Martinique, ×3.1, ×3.7, respectively.

1 

2 

3 

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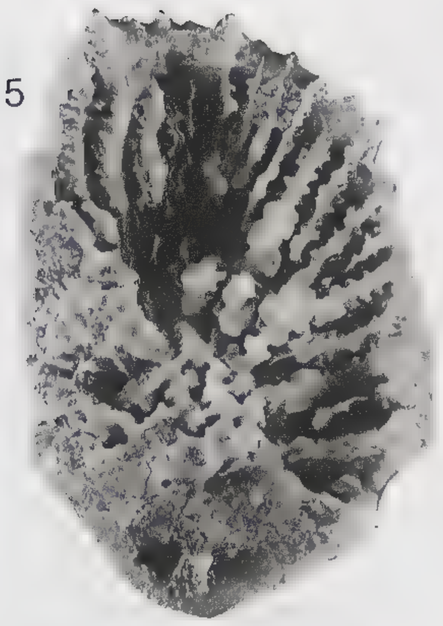
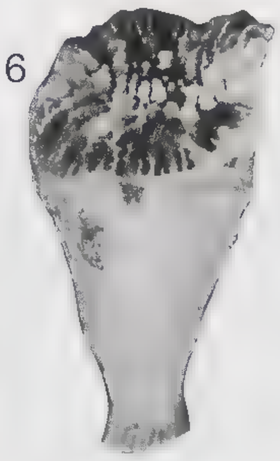
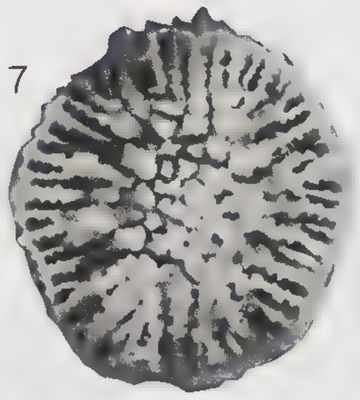
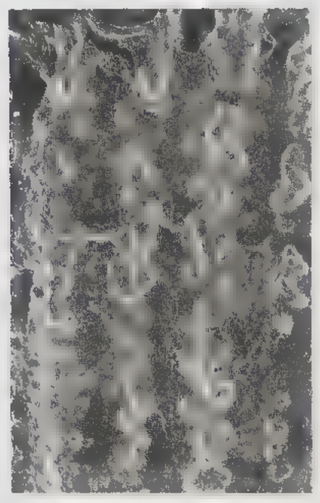
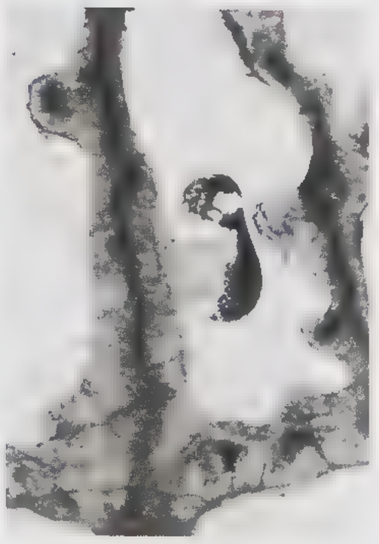
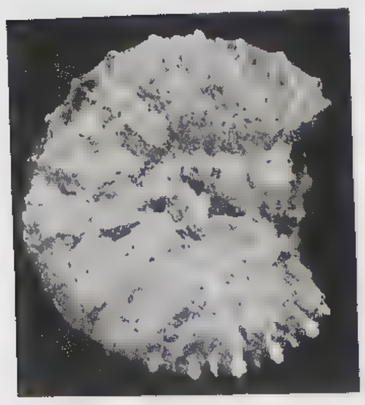
5 

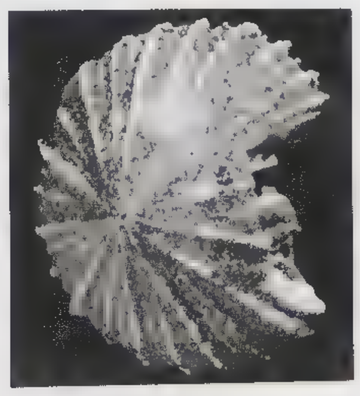
6 

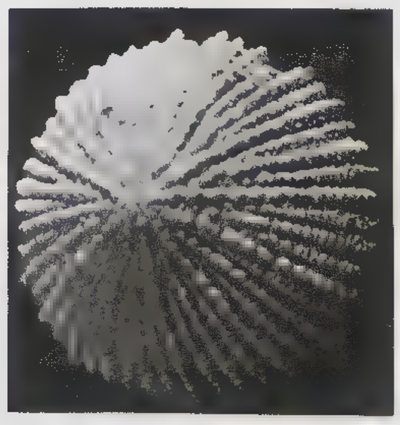
7 

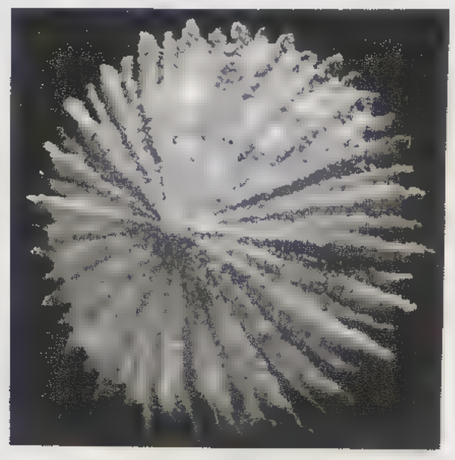
8 

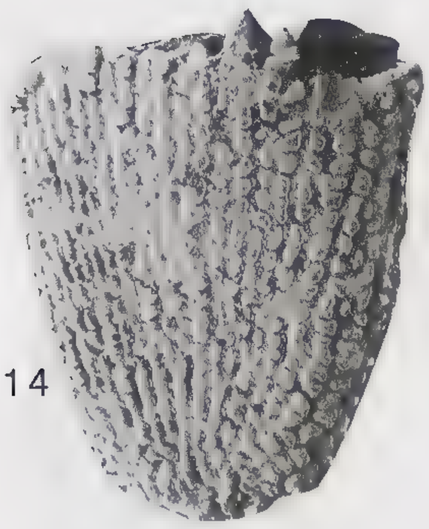
9 

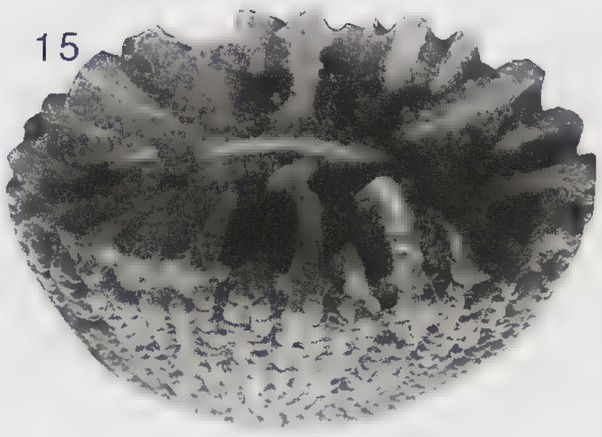
10 

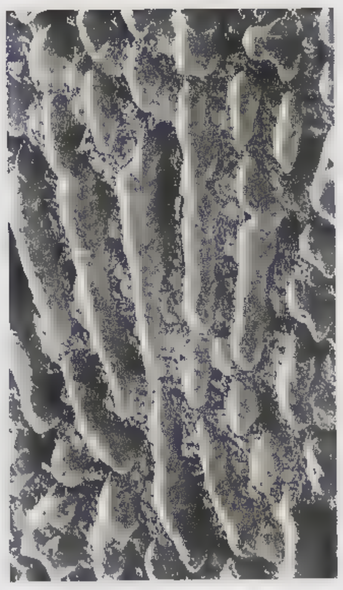
11 

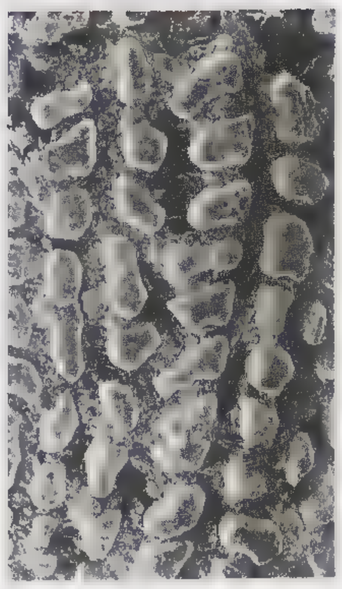
12 

13 

14 

15 

16 

17 

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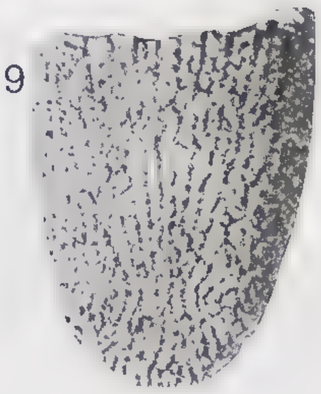
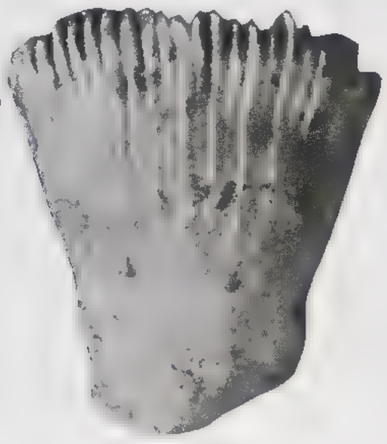
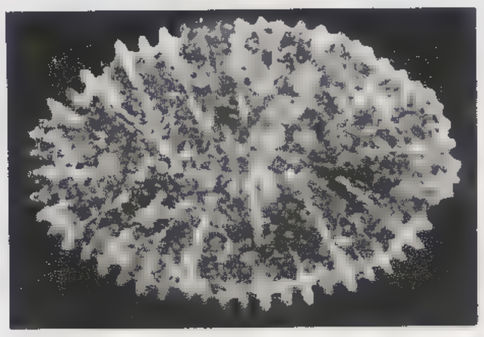
19 

20 

21 

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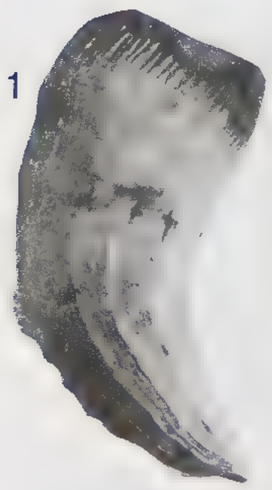

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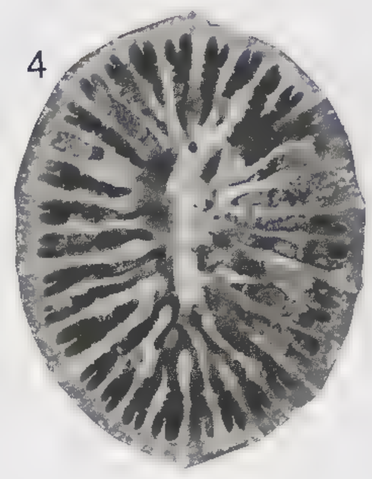

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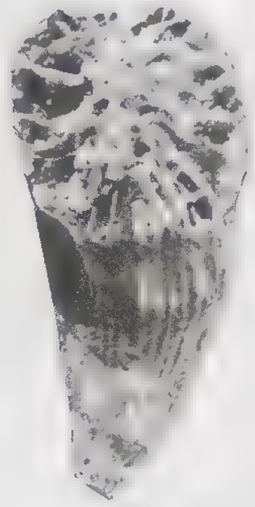

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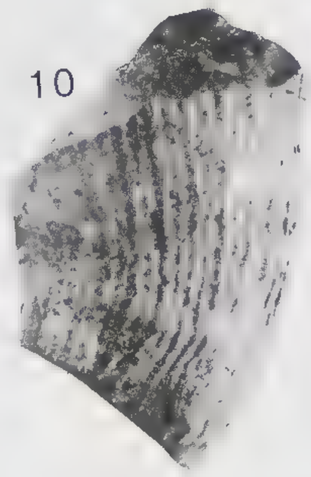

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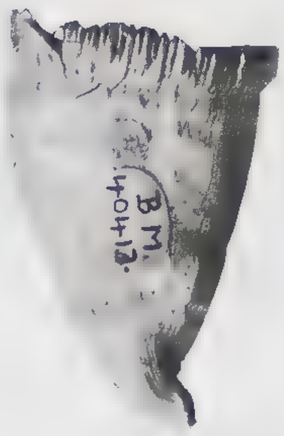

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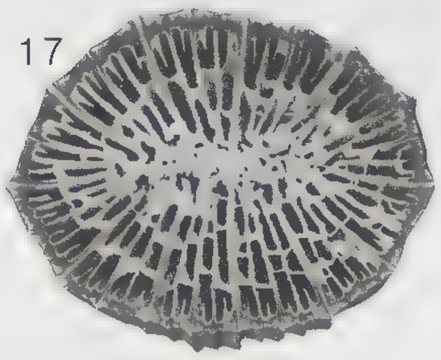

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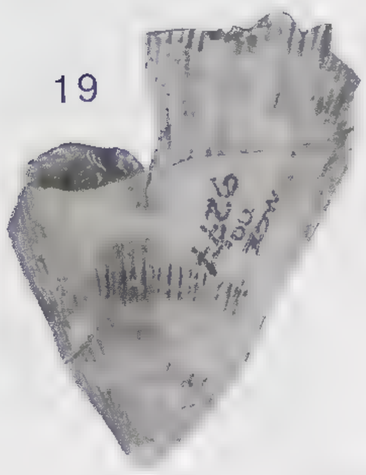

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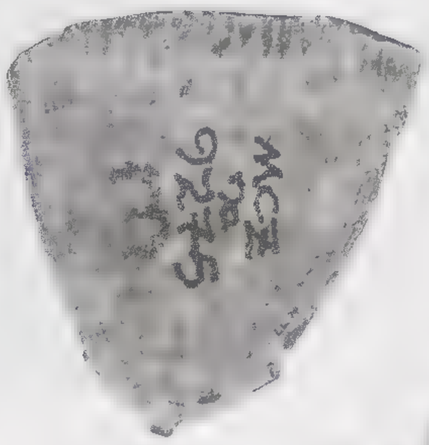

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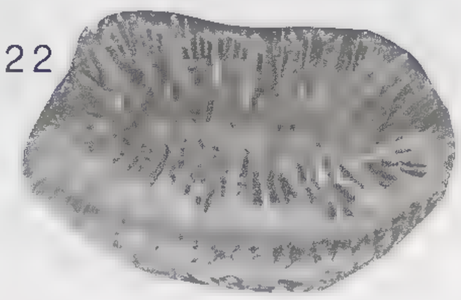

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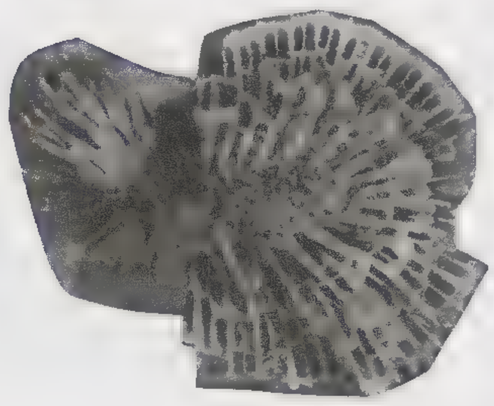

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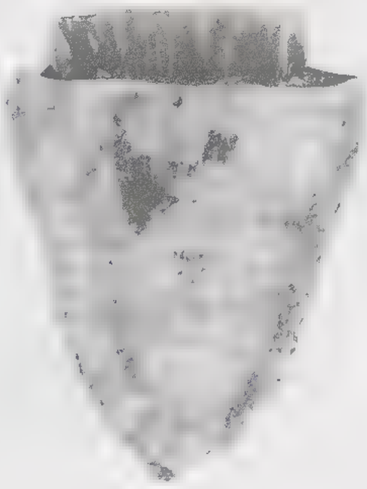

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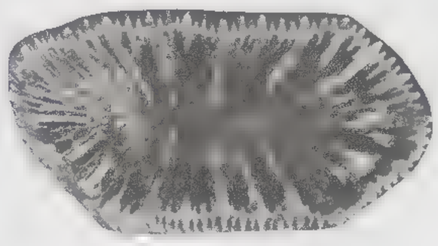

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1–4, 6. ***Asterosmilia abnormalis*** (Duncan, 1864) 37

1. Side view of specimen (USNM 546427) showing alate costa on convex lateral edge, ×1.3. Loc. USGS 8519.

2, 3. Duncan's illustrated syntype [BM(NH) 28801], both faces figured, ×1.1.

4. Damaged calice of specimen (USNM 546424) from Loc. USGS 8519, ×3.2.

6. Transverse thin-section of calice (NMB D5893) showing theca and three septa, ×20. Loc. NMB 16910.

5. ***Asterosmilia prolifera*** (Pourtalès, 1871) 37

Recent specimen (USNM 74687) from *R/V Silver Bay* sta. 2445: 24°08′N, 80°08′W, 252 m, 3 Nov. 1960, ×1.0.

7–9, 11. ***Asterosmilia exarata*** Duncan, 1867 38

7, 8. Side and calicular views of largest syntype (USNM 324816) of *A. hilli* Vaughan, 1919, ×1.6, ×2.0, respectively. Loc. USGS 2580.

9. Holotype [BM(NH) R28944] of *A. exarata,* ×2.2. Specimen figured by Duncan, 1867, pl. 32, fig. 5.

11. Longitudinal fracture of specimen (USNM 63329) from Loc. USGS 2580 (Jamaica) showing dissepiments, ×2.4.

10. ***Asterosmilia*** species cf. ***A. hilli*** of Wells, 1934 39

Specimen (USNM 44303) reported by Wells (1934) from the Scotland Beds of Barbados, ×3.4.

12–18. ***Asterosmilia profunda*** (Duncan, 1864) 39

12. SEM of longitudinal fracture through specimen (USNM 546424) showing two dissepiments, ×12.4. Loc. USGS 8528.

13. Elongate corallum (USNM 63327) from Loc. USGS 2580 (Jamaica), ×0.5.

14, 15. Side and calicular views of holotype [BM(NH) 40413], ×0.88, ×1.4, respectively.

16. Longitudinal cut of specimen (NMB D5894) from Loc. NMB 15833 revealing dissepiments, ×1.3.

17. Transverse cut of specimen (USNM 63327) from Loc. USGS 2580 (Jamaica) revealing abundant dissepiments, ×2.8.

18. Transverse thin section through two septa and wall of specimen (NMB D5895), ×12. Loc. NMB 15833.

19, 20. ***Asterosmilia duncani*** Vaughan, 1925 40

Side and calicular views of holotype (MCZ 9277), ×1.1, ×1.4, respectively.

21–24. ***Asterosmilia compressa*** Vaughan, 1925 40

21, 22. Side and calicular views of syntype (MCZ 9275), ×1.4.

23. Side view of syntype (MCZ 9276), ×2.2.

24. Calice of syntype (MCZ 9273), ×1.6.

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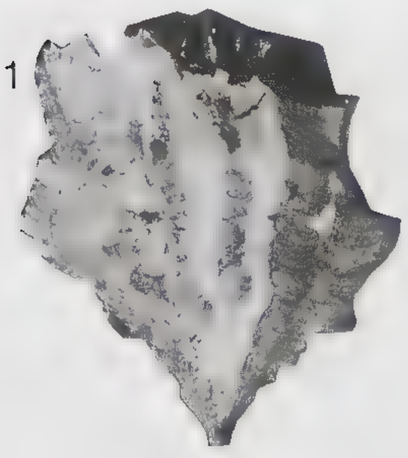
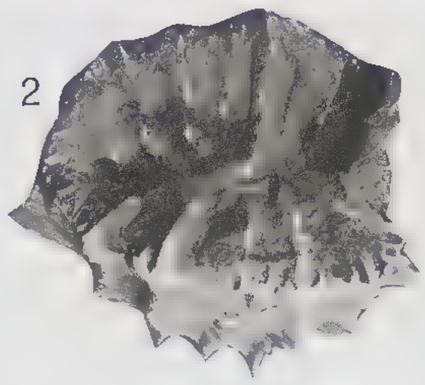
1, 2. ?***Flabellum*** species 41
Side and calicular views of specimen (USNM 64202) from Loc. USGS 8733, ×1.4.

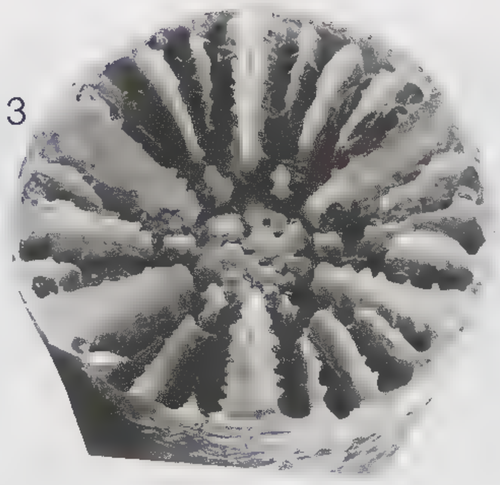
3–7, 10, 11. ***Pourtalocyathus hispidus*** (Pourtalès, 1878) 41
3. SEM of well-preserved calice (USNM 74688) showing three cycles of septa, columella, and pali, ×12.5. Loc. TU 1227A.
4. SEM side view of upper theca of specimen (USNM 74688) showing smooth concentric banding of epitheca (see also Pl. 11, fig. 3), ×16.4. Loc. TU 1227A.
5. Transverse thin-section through three septa of calice (USNM 61928), ×62. *R/V Caroline* sta. 67: 18°32′18″N, 65°46′12″W, 329–512 m, Recent.
6. SEM of septal granules in specimen (USNM 74688), ×145. Loc. TU 1227A.
7. Stereo SEM of well-preserved corallum (USNM 74688), ×9.4. Loc. TU 1227A.
10, 11. Rows of mural pores in specimen (NMB D5896), ×15.3, ×65, respectively. Loc. NMB 16038.

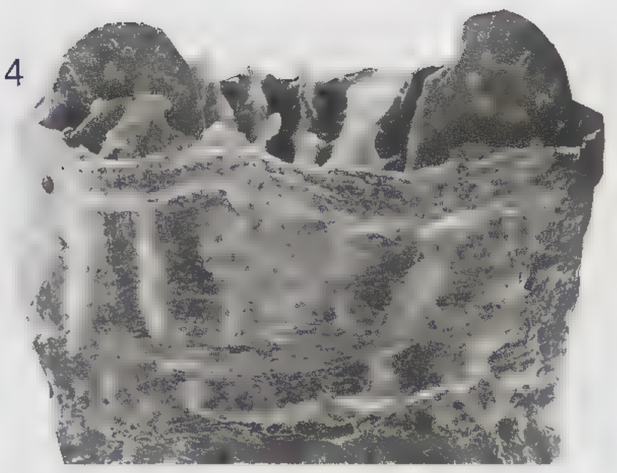
8, 9, 12, 13. ***Guynia*** species cf. ***G. annulata*** Duncan, 1872 42
8, 12, 13. Theca (USNM 74689) showing costal spines, ×33, ×65, ×21, respectively. Loc. TU 1227A.
9. Calice of specimen (USNM 74689) showing octameral symmetry (see also Pl. 11, figs. 8, 12, 13), ×38.

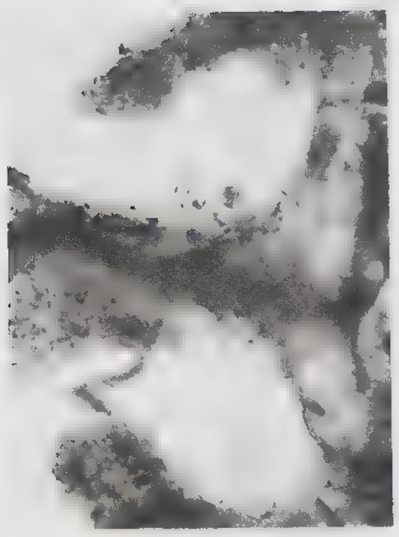
14–17. ***Dendrophyllia cornucopia*** Pourtalès, 1871 43
14. Recent specimen (USNM 46685) from Straits of Florida: 24°18.7′N, 81°56.9′W, 220 m, ×0.64.
15–17. Side and calicular views of specimens (USNM 64227) from Loc. USGS 8528, ×1.3, ×2.4, ×2.4, respectively.

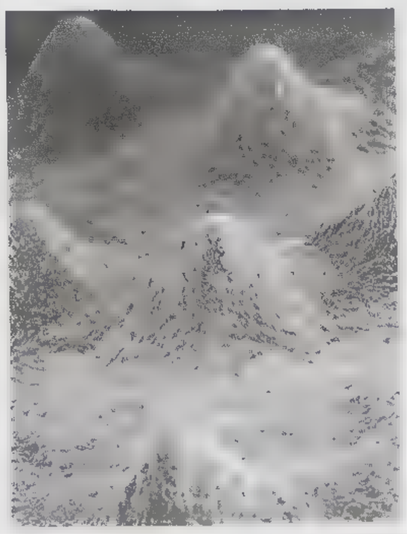
1 

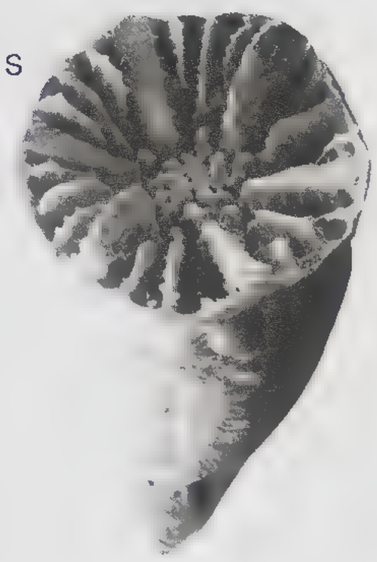
2 

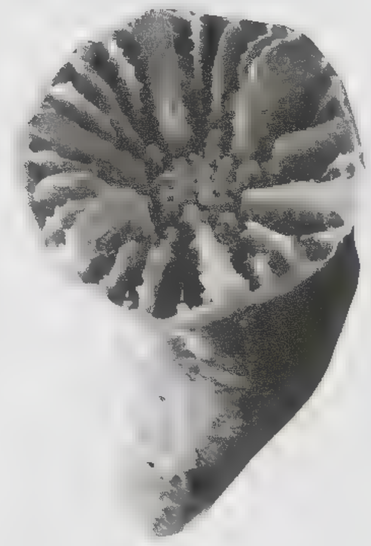
3 

4 

5 

6 

7s 



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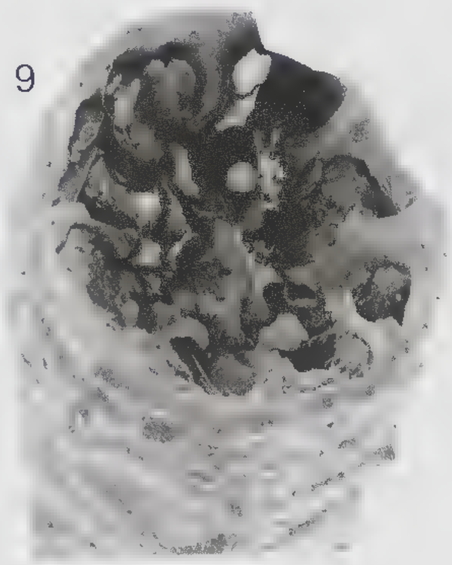
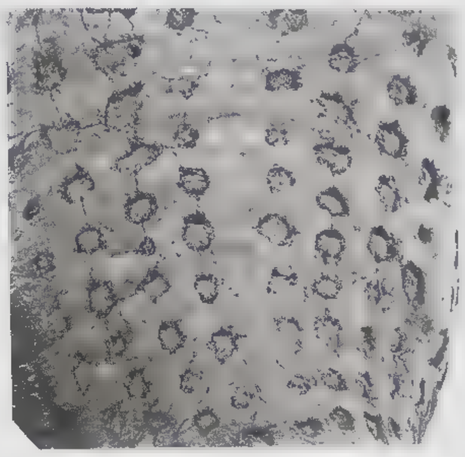
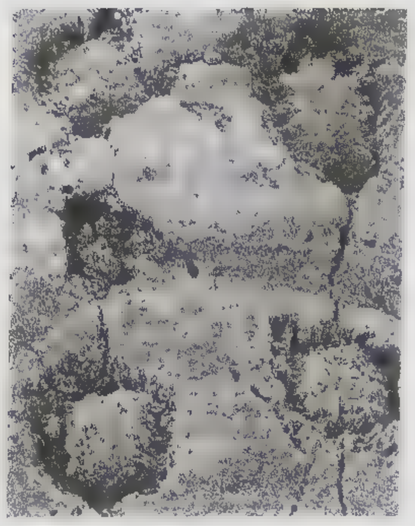
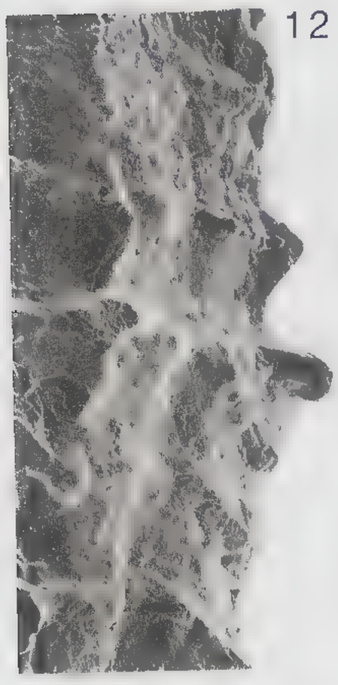
9 

10 

11 

12 

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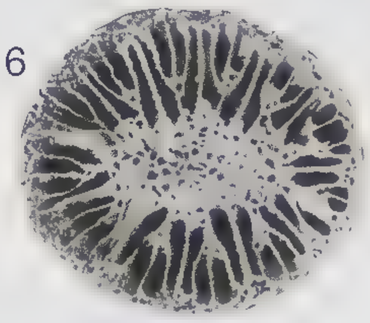
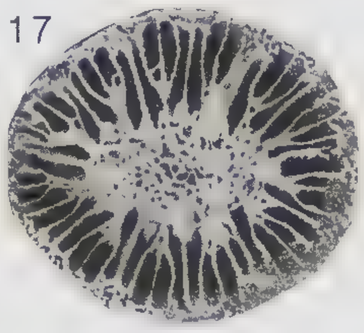
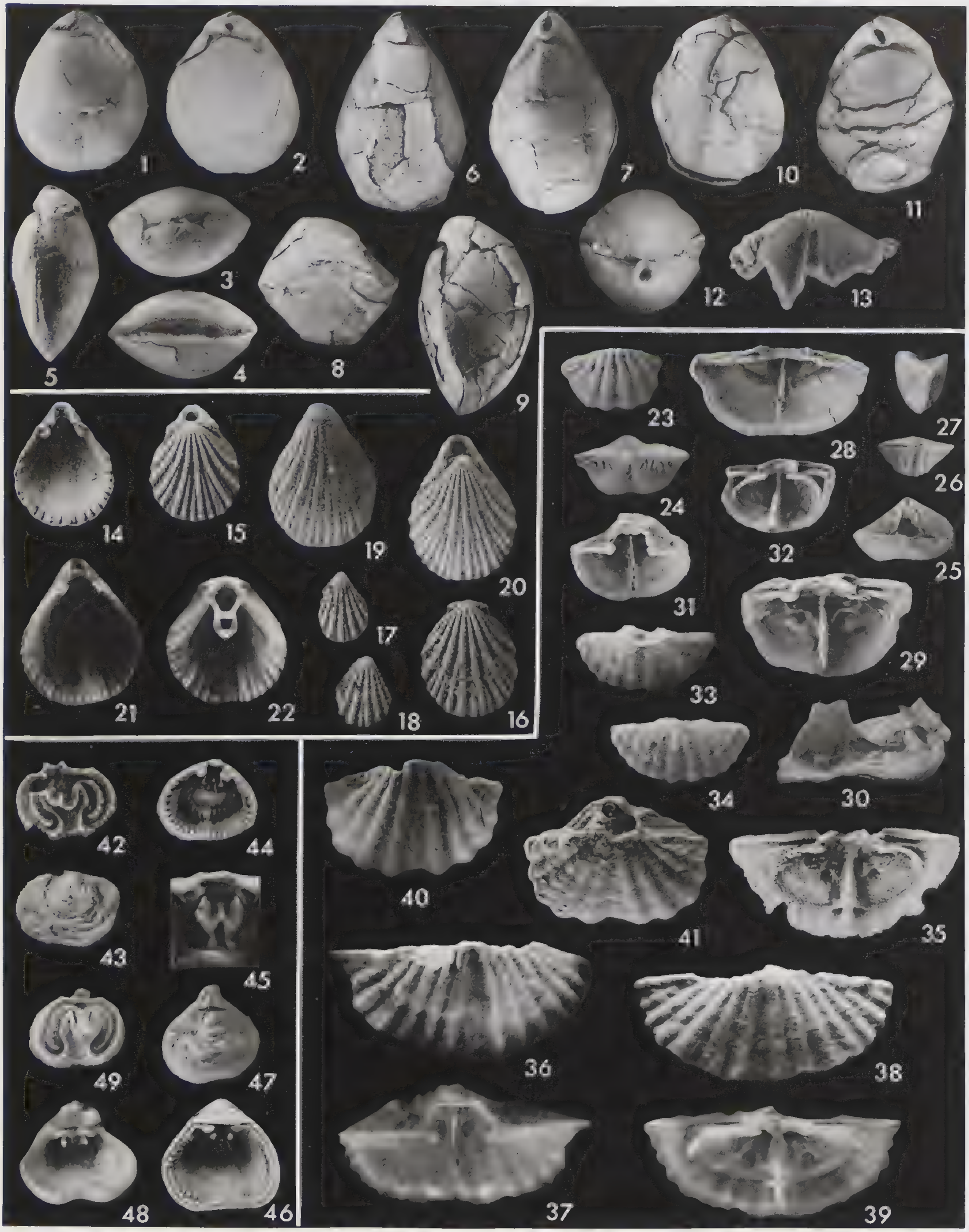
16 

17 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EXPLANATION OF PLATE 12

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1–13. ***Tichosina*? *lecta*** (Guppy) 48

1–5. Pedicle valve, brachial valve, posterior margin, anterior margin and side views of a complete specimen, ×1, hypotype USNM 410560, Mao Formation, Río Gurabo section, locality TU 1300.

6–9. Pedicle valve, brachial valve, anterior margin and side views of a distorted complete specimen, showing resemblance to *T.*? *bartletti* (Dall), ×1, hypotype USNM 410561, Mao Formation, Río Gurabo section, locality TU 1300.

10, 11. Pedicle and brachial valves of a partially-crushed example, ×1, hypotype USNM 410562, Mao Formation, Río Gurabo section, locality TU 1300.

12. Posterior margin, showing labiate foramen, ×1, hypotype USNM 410563, ×1, Mao Formation, Río Cana section, locality NMB 16884.

13. Enlargement of crural bases of brachial valve, ×5, hypotype USNM 410564, Mao Formation, Río Gurabo section, locality NMB 15828.

14–22. ***Terebratulina cailleti*** Crosse 49

14. Pedicle valve interior, ×4, hypotype USNM 410566, Mao Formation, Río Cana section, locality NMB 17023.

15. Brachial valve view of complete specimen, ×4, hypotype USNM 410567, Mao Formation, Río Cana section, locality NMB 17023.

16. Brachial valve exterior, ×4, hypotype USNM 410565, Mao Formation, Río Cana section, locality NMB 16884.

17, 18. Brachial valve exteriors, ×4, hypotypes USNM 410568 and 410569, respectively, Mao Formation, Río Cana section, locality NMB 17023.

19, 20. Pedicle and brachial valve views of a complete specimen, ×4, hypotype USNM 410570, Recent, off Paynes Bay, Barbados, dredged from 125–150 m.

21, 22. Pedicle and brachial valve interiors of a complete specimen, ×4, hypotype USNM 410571, Recent, off Paynes Bay, Barbados, dredged from 125–150 m.

23–41. ***Argyrotheca johnsoni*** Cooper 50

23. Pedicle valve, ×5, hypotype USNM 410572, Mao Formation, Río Cana section, locality NMB 17023.

24. Posterior view of complete specimen, ×4, hypotype USNM 410573, Gurabo Formation, Río Gurabo section, locality NMB 15840.

25. Posterior margin of complete specimen, ×5, hypotype USNM 410574, Gurabo Formation, Río Gurabo section, locality NMB 15838.

26. Anterior margin of complete specimen, hypotype USNM 410575, ×5, Gurabo Formation, Río Gurabo section, locality NMB 15823.

27. Side view of complete specimen, hypotype USNM 410576, ×5, Gurabo Formation, Río Gurabo section, locality NMB 15823.

28–30. Pedicle and brachial valve interiors, ×6, and SEM profile of median septum of brachial valve, ×10, hypotype USNM 410577, Gurabo Formation, Río Gurabo section, locality NMB 15942.

31, 32. Pedicle and brachial valve interiors of a complete specimen, ×6, hypotype USNM 410578, Mao Formation, Río Cana section, locality NMB 16884.

33, 34. Pedicle and brachial valves of an alate complete specimen, ×6, hypotype USNM 410579, Gurabo Formation, Río Gurabo section, locality TU 1215.

35. Brachial valve interior, ×12, hypotpye USNM 410580, Gurabo Formation, Río Gurabo section, locality NMB 15853.

36–39. External and internal views of a complete alate specimen, ×6, hypotpye USNM 410581 (out of USNM lot No. 549947), Recent, off Cape Samaná, Dominican Republic, dredged from 75 m depth.

40, 41. Pedicle and brachial valves of a complete specimen, ×5, hypotype USNM 410582 (out of USNM lot No. 549947), Recent, off Cape Samaná, Dominican Republic, dredged from 75 m depth.

42–49. ***Lacazella caribbeanensis*** Cooper 51

42. Brachial valve interior of partially-worn specimen, ×8, hypotype USNM 410583, Gurabo Formation, Río Gurabo section, locality NMB 15942.

43. Brachial valve exterior, hypotype USNM 410584, Gurabo Formation, Río Gurabo section, locality TU 1211.

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46. Pedicle valve interior, ×8, hypotype USNM 410586, Recent, attached to stalagmite in blue hole off South Bight, Andros Island, Bahamas, at depth of 45 m.

47. Brachial valve of complete specimen, ×5, hypotype USNM 250952, Recent, Grand Bahama Island, Bahamas, 20 m depth.

48. Pedicle valve interior, tilted to show hemispondylium, ×6, hypotpye USNM 250983, Recent, Grand Bahama Island, Bahamas, 20 m depth.

49. Brachial valve interior, ×5, hypotype USNM 250984, Recent, Grand Bahama Island, Bahamas, 20 m depth.

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